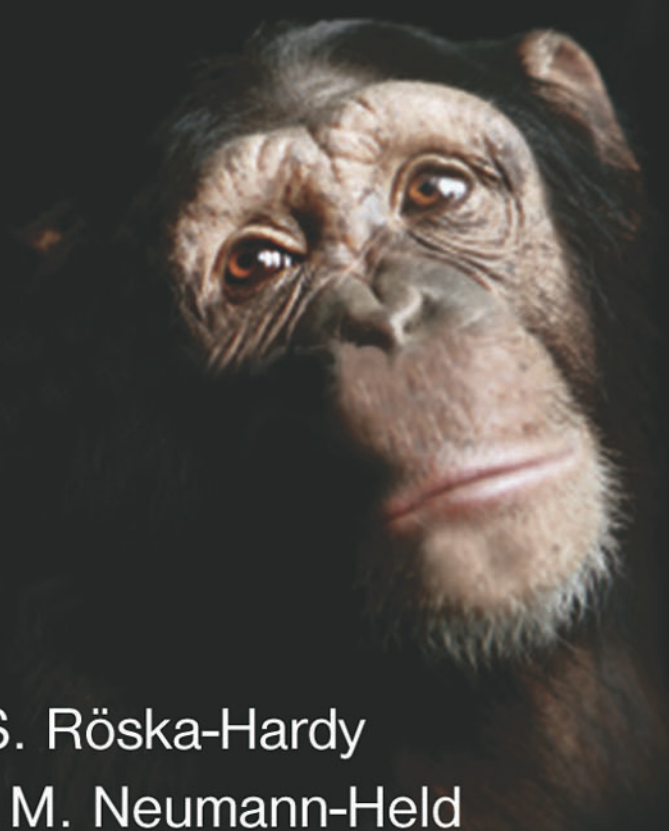# Learning from Animals?

Examining the Nature of Human Uniqueness

Edited by

Louise S. Röska-Hardy
and Eva M. Neumann-Held

Learning from Animals?

Human language, cognition, and culture are unique; they are unparalleled in the animal kingdom. The claim that we can learn what makes us human by studying other animal species provokes vigorous reactions and many deny that comparative research can shed any light on the origins and character of human distinctive capacities. However, *Learning from Animals?* presents empirical research and an analysis of comparative approaches for an understanding of human uniqueness, arguing that we cannot know what capacities are uniquely human until we learn what other species can do.

This interdisciplinary volume explores the prospects and problems of comparative approaches for understanding modern humans' abilities by presenting: (1) the latest findings and theoretical approaches in primatology, comparative psychology, linguistics, and philosophy; (2) methodological reflections on the prospects and challenges of understanding human capacities through comparative research strategies; and (3) discussions of conceptual and ethical issues.

This is the first book to address the issues raised by comparative research from such a diverse perspective. It will therefore be of great interest to students, researchers, and professionals in comparative psychology, linguistics, primatology, biology, and philosophy.

Louise S. Röska-Hardy studied philosophy and linguistics, before taking her doctorate in philosophy, sociology, and linguistics in Frankfurt am Main. She has taught philosophy and linguistics at universities in Germany, Switzerland, and the USA.

Eva M. Neumann-Held studied biology and philosophy. As researcher and lecturer she participated in numerous biophilosophical projects, among them "Genome and Organisms: Philosophical Interpretations of Developmental Biology". Currently she lectures in philosophy and biophilosophy at the University of Witten-Herdecke, Germany.

Röska-Hardy and Neumann-Held are among the founders of the interdisciplinary research group "What are Human Beings? Culture—Language—Nature" (University of Dortmund and KWI).

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Contributors

Kim A. Bard (PhD) is Director at the Centre for the Study of Emotion, and Professor of Comparative Developmental Psychology at the Department of Psychology, University of Portsmouth, UK.

Ingar Brinck (PhD) is a Senior Lecturer and Research Fellow in theoretical philosophy at the Department of Philosophy and Cognitive Science, Lund University, Lund, Sweden.

Judith-Maria Burkart (PhD) is a Senior Lecturer at the Anthropological Institute and Museum, University of Zürich, Switzerland.

Christine A. Caldwell (PhD) is a Lecturer in Psychology at the University of Stirling, UK.

Josep Call (PhD) is Director of the Wolfgang Köhler Primate Research Center, and a Senior Scientist at the Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

W. Tecumseh Fitch (PhD) is a Reader at the School of Psychology and the Centre for Social Learning and Cognitive Evolution, University of St. Andrews, Scotland, UK.

Ludwig Huber (PhD) is an Associate Professor, Lecturer, and Director of the Cognition Lab in the Department for Neurobiology and Cognition Research, University of Vienna, Austria.

Dale Jamieson (PhD) is Director of Environmental Studies, and also Professor of Environmental Studies and Philosophy, and Affiliated Professor of Law, New York University, USA.

Matthias Kettner (PhD) is Professor of Philosophy and Director of Research, Witten/Herdecke University, Witten, Germany.

David A. Leavens (PhD) is a Senior Lecturer in Psychology at the Department of Psychology in the School of Life Sciences, University of Sussex, Falmer, UK.

William C. McGrew (PhD) is a Lecturer in the Department of Biological

Anthropology, Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, UK.

Adrien Meguerditchian (MSc) is a Research Associate at the Yerkes Primate Center, Atlanta, USA, and also at the Research Centre in the Psychology of Cognition, Language and Emotion at the University of Provence, Aix-en-Provence, France.

Eva M. Neumann-Held (PhD) is an Instructor at the Witten/Herdecke University, Witten, Germany.

Hannes Rakoczy (PhD) is a Postdoctoral Researcher in the Department of Developmental and Comparative Psychology at the Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

Friederike Range (PhD) is a Director of the Wolf Science Center, Grünau, Austria and a Postdoctoral Researcher in the Cognition Lab at the Department for Neurobiology and Cognition Research, University of Vienna, Austria.

Louise S. Röska-Hardy (PhD) is a Research Fellow at the Institute for Advanced Study in the Humanities, Essen, Germany.

Jacques Vauclair (PhD) is Director of the Research Centre in the Psychology of Cognition, Language and Emotion, and a Professor in the Department of Developmental and Comparative Psychology at the University of Provence, Aix-en-Provence, France.

Zsófia Virányi (PhD) is a Director of the Wolf Science Center, Grünau, Austria and a Postdoctoral Researcher at the Konrad Lorenz Institute for Evolution and Cognition Research, Altenberg, Austria.

Wolfgang Wildgen (PhD) is Professor in the Department of Germanic Linguistics and Literature, University of Bremen, Germany.

Foreword

Josep Call

This book explores the question of whether we can learn about human behaviour and cognition by studying nonhuman animals. It is interesting that the title of the book does not present a conclusive statement, instead it poses a question: *Learning from Animals?* I think that this is an excellent choice because readers may not only agree or disagree with the arguments presented throughout the various chapters but also, and perhaps more revealing, they may disagree on the need for the question mark at the end of the title. Such a disagreement over a seemingly insignificant punctuation mark highlights the clash between two deeply rooted intellectual traditions regarding the place of humans in nature and their relation to other living organisms. One tradition emphasizes continuity and the other tradition emphasizes discontinuity.

For those readers interested in evolution, and human evolution in particular, the behaviour of nonhuman animals is very informative. Since we cannot go back in time and certain traits such as behaviour and cognition do not fossilize, comparing those traits across a variety of extant species is one of the main tools that we have at our disposal to make inferences about the evolution of those traits. This is not a foolproof method but at least it can give us some hints about how certain traits may have evolved.

But even leaving evolutionary issues aside, it is useful to compare species because contrast often leads to discovery. In effect, it is relatively easy to document what a species does, but it is much harder to document what it does not do. After all, every species does not do an infinite number of things and it is not a trivial matter to decide which omissions are significant and which ones are not. Those omissions only become apparent after studying another species that display precisely those traits. Although such a procedure may seem obvious, quite often we have defined what makes us human by solely studying humans, without comparing our behaviour with that of other species.

It is partly understandable that scholars devoted to the study of complex human activities such as the global market economy, marriage rituals, and international law may be sceptical about the contribution that animal work can make to their respective fields of expertise. After all, animals do not do anything resembling those activities and, consequently, scholars may choose

to focus on humans directly. Note, however, that 50 years ago we may have included in the list of complex and uniquely human activities things like material culture and language, but as several chapters in this book nicely illustrate, there is a lot to be learned from animals precisely about those areas. I would invite sceptics to read this book—they will find some useful insights in it. This is not to say that the chapters in this book prove that nonhuman animals have language or material culture in the human sense. If this is what readers are expecting to find, they will not find it here. What the reader may find is what I would call elements of culture or elements of language. But identifying those elements is already a big first step in the right direction that can contribute decisively to the establishment of bridges between scholars of different intellectual traditions.

Another important step needed to foster the exchange of ideas between traditions consists of critically evaluating our own positions as well as those of our intellectual neighbours. For the proponents of continuity, it is easy to get carried away by the similarities between humans and nonhumans (particularly with regard to the great apes) that have been discovered in the last few decades and downplay the differences. The combative stance of some of the proponents of the continuity view is quite understandable if one thinks that they have been fighting against a deeply entrenched tradition of human uniqueness too often based on a very shaky (or simply nonexistent) empirical foundation. However, continuity proponents should be mindful that attaching labels, typically used to describe human activities, to the behaviour of nonhuman animals in an attempt to "bridge the gap" while sweeping under the rug the important differences that may exist may not be very helpful. No matter what things are called, their nature will remain the same and using the same label for two different things simply creates confusion. For the proponents of the discontinuous view, it is all too easy to forget about some of the deeply rooted similarities that exist between humans and nonhuman animals. Under the deceptive outer skin provided by our cultural practices run some striking similarities between humans and nonhuman animals that too often have not received the attention that they deserve.

I am convinced that scholars in the continuity and discontinuity traditions recognize that there are both similarities and differences between humans and nonhuman animals. Where they disagree is on where exactly the differences (and similarities) lie and how large those differences (and similarities) are. Unfortunately, much too often, debates between traditions are the exception rather than the norm, particularly when they cross discipline boundaries. It is precisely at this junction that this book has a lot to offer because it can highlight both the similarities and the differences between humans and nonhuman animals. More importantly, it can contribute to reaching a much needed balance between the two intellectual traditions. Although this may seem an obvious thing to say, given how hard this balance is to achieve (and some chapters are very illustrative on this point), I feel that we all (myself included) need some reminding of this fact from time to time.

Acknowledgements

Introduction—Issues and themes in comparative studies

Language, cognition, and culture

Louise S. Röska-Hardy

Anyone seeking to understand humans' place in nature is faced with an explanatory challenge where human language, cognition, and culture are concerned, especially within an evolutionary perspective. These human capacities are not just distinctive; they are apparently unparalleled in the animal kingdom. No other known species communicates by means of a system with the features of human language. Language enables us to produce novel utterances that others can understand and lets us offload information onto artifacts like note paper and computers. It allows us to talk about the past and the future, to refer to things that are physically distant and to things that do not exist. Importantly, language allows humans to influence and affect the cognition and the culture of other humans by symbolic means—a feat unequalled among other animals.

Typically human cognition exhibits a degree of plasticity and forms of social cognition that have not been found in any other species. The human capacity to learn is remarkable for the complexity and difficulty of what can be learned as well as for the speed of learning. Like other social species, humans map the social world, but they focus on the activities of conspecifics in a distinctive way. They come to interpret and anticipate others' actions not merely on the basis of past cooperation and competition, but in terms of networks of psychological states like belief and intention. Moreover, humans can explicitly think about thinking, enabling higher order thought as well as metarepresentational knowledge and metacognitive regulation. At the same time, human cognition is profoundly influenced by the social and cultural contexts provided by other humans, i.e., by the concepts, skills, and artifacts conveyed in language and culture.

Human culture exhibits a behavioural and cognitive differentiation or flexibility that outstrips that of animal traditions or "cultures", as writing systems, opera, and aeronautical engineering testify. The transmission of human culture is characterized by full-fledged imitation that allows for the cumulative improvement of innovation as well as by explicit teaching or pedagogy. Through culture humans actively modify and scaffold their environment to suit their purposes and support their aims. Their cultural skills and artifacts enable them to overcome physical, cognitive, and geographical

limitations, e.g., with aeroplanes and the Internet, and to influence the development of individuals' capacities directly through education. As a consequence, the human capacity for culture has transformed the relationship between humans and their environment so that humans' situation differs significantly from that of any other animal species.

Humans are thus unique in nature—both in respect of what it is to be human and in respect to the rest of nature. Nonetheless, humans are only one of many species. Thus, from an evolutionary perspective the challenge is to place the species-unique capacities of humans in an evolutionary context. This entails developing conjectures about possible precursors to human traits and hypotheses about the evolutionary paths that led to modern humans' capacities. One central question is whether human-specific traits lie on a continuum with those of nonhuman animal species or whether they are essentially different, i.e., discontinuous. One way to approach this question is to investigate in which respects humans and nonhuman animals resemble each other and how they differ.

In the past decade comparative studies of humans and nonhuman animals have generated a wealth of findings, which bear on questions concerning the evolution of language, the nature of primate cognition, and the roots of culture. However, the importance of these studies for an understanding of human uniqueness is controversial. Human language, cognition, and culture seem so different from the capacities of other species that there is a question as to what we can discover about humans' unique capacities from research on nonhuman animals. Can we find out what makes us uniquely human by studying other animals?

This multidisciplinary volume explores the question by presenting original comparative research in tandem with critical reflection on the significance of comparative studies, broadly construed, for an understanding of human uniqueness. The chapters are authored by linguists, psychologists, primatologists, cognitive ethologists, and philosophers who have pursued a comparative approach and addressed the related disciplinary debates in their research. The contributors have been selected in order to highlight key debates and to illustrate different comparative approaches in established fields of research as well as in emerging fields such as biolinguistics. All share the evolutionary assumption that human language, cognition, and culture did not arise *de novo*. Nevertheless, they differ over whether these human traits reflect the gradual elaboration and extension of antecedents found in other animals along a continuous pathway or whether they point to singular, uniquely human adaptations that mark a discontinuity in the evolution of human capacities from those of animal predecessors. Consequently, the chapters represent diverse and often competing positions on the issue of continuity versus discontinuity in evolutionary paths.

This chapter introduces the major issues in the debate over the significance of comparative research. It outlines the competing theoretical paradigms and methodological approaches, pointing out their presuppositions and

limitations. The main issues in current disciplinary debates on language, cognition, and culture are then presented and discussed with reference to the individual chapters. A guiding assumption is that human uniqueness will be better understood if we can situate humans' species-unique capacities within an evolutionary framework. This notion contrasts with a deeply rooted view of the nature of human uniqueness.

The human capacities for language, cognition, and culture along with the reciprocal relationships among them are often taken to imply an unbridgeable divide, a categorical difference between humans and other animals. In Western thought, religious worldviews and philosophical doctrines have posited a radical dichotomy or an ontological difference between humans and other species, characterizing humans as "the pinnacle of creation" and animals as "mindless brutes". Aristotle's idea of a *scala naturae*, a ladder of nature progressing from "lower" to "higher" forms of life, and its medieval and nineteenth-century interpretation in "the Great Chain of Being" are still influential today. The traces of this pre-Darwinian view are evident in the lay public's view of the relation between humans and other species and can be found in popularizations of evolutionary theory that portray evolution as a linear progression from "lower" to "superior" species that "culminates" in modern humans.

In the twenty-first century it is difficult to defend any view of human uniqueness that refuses to consider the findings of natural science and wellfounded evolutionary hypotheses concerning the development of the human species from animal predecessors. In the modern evolutionary perspective the idea of a linear *scala naturae* is replaced by a Darwinian tree, which branches out and ramifies over time as a result of different evolutionary processes. In this view contemporary species evolved from earlier ones by adaptation, e.g., as a result of natural selection operating on genetic variation, and by processes of evolutionary selection involving variation and selective retention in the face of environmental pressures. From an evolutionary standpoint *all* species are unique in that they have developed distinctive capacities to solve the problems that emerged in their evolutionary past. On this understanding, human language, cognition, and culture are unique by definition. But, equally, many capacities of other animals are unique, too, e.g., echolocation in bats and dolphins. This prompts the question of how species-unique human capacities relate to those of other animals as they must on any evolutionary view.

In a broad evolutionary perspective the question of human uniqueness concerns the nature of our species-typical traits, the human phenotype, and how these behavioural and cognitive traits arose over evolutionary time. There is, however, a further aspect of human uniqueness which stems from humans' ability to inquire into their own nature and existence. Endowed with linguistic and reflective cognitive capacities and with a sense of past, present, and future, we humans are in a position to raise and to explore the question of our own origins. In our attempts to understand human evolution and

existence, we naturally start from an anthropocentric perspective, comparing other species' abilities to our own in order to better understand our specific capacities and their place in nature. However, this does not entail taking humans and their typical abilities to be "the measure of all things" in Protagoras' phrase. Rather, from our natural anthropocentric perspective we seek to place the capacities of modern humans, *Homo sapiens sapiens*, in an evolutionary context. This requires integrating knowledge from disparate sources and different disciplines. It is no mean task and of necessity multidisciplinary.

On the assumption that modern humans' capacities were shaped by their evolutionary past, an in-depth understanding of human uniqueness would describe possible adaptations and mechanisms that provided precursors to our species-specific capacities. If we can tease out the mechanisms and precursors from which these capacities evolved, we will presumably obtain a better understanding of their nature and relationships to the abilities of living nonhuman animals. This suggests that an answer to the question of human uniqueness is contingent on our discerning how human capacities resemble and differ from those of other animals and on our ability to reconstruct the possible evolutionary paths by which we became human. Making progress along these lines would tell us more about what it is to be human and at the same time deepen our understanding of our relation to the rest of nature. The difficulties inherent in achieving such an understanding are formidable and whether the undertaking is possible is itself a matter of debate.

Since there are no extant species ancestral to any living species, i.e., all direct ancestors are extinct, the evolutionary history of a trait must be inferred from contemporary sources of evidence, e.g., genetic and biochemical analyses, the fossil record, or comparisons with other surviving species. Over the past decades genetic analyses of DNA sequences have provided an important source of data for inferring relationships between different species. However, the exact pathways from genotype to phenotype, from DNA sequences to higher level traits like language or cognition, are complex and largely uncharted. Additional factors appear to play an important, intervening role, e.g., epigenetic factors, experience-dependent modifications of postnatal brain development (Jablonka & Lamb, 2007). For example, the genomes of *Homo sapiens sapiens* and the closest living evolutionary relative, the chimpanzee, *Pan troglodytes*, exhibit striking similarities at the level of DNA sequences, while the respective phenotypes differ markedly. This suggests that additional sources of evidence are necessary in order to relate genetic differences to specific phenotypical traits.

The fossil record provides a second source of information on the evolutionary history of traits. Fossils can yield information about the order in which different traits arose during phylogeny, the evolutionary history of species, e.g., increased brain size and bipedalism in hominid evolution. They also provide information on the associated timeline, thus placing constraints on evolutionary hypotheses. However, the fossil record is fragmentary and

incomplete. We cannot assume that fossils from all stages in the evolution of a species have been preserved or that they will be found. In particular, capacities like language and species-typical cognition do not fossilize. Since language and cognition leave no trace in the fossil record and artifacts testify only indirectly to the presence of culture, not to its nature, we must look to other sources to develop hypotheses concerning evolutionary pathways.

The comparative, empirical study of living animals offers a third approach to tracing the phylogeny of surviving species and the evolutionary roots of their characteristics. From an evolutionary perspective there is good reason to expect comparisons among animal species to suggest hypotheses concerning the phylogeny of human and nonhuman animal traits and the sequence of evolutionary changes that shaped them. First, comparisons of phylogenetically close species support conjectures about the presence or absence of particular traits in common ancestors. Accordingly, comparisons between humans and closely related species like the great apes may provide information about precursors to human capacities on the basis of descent from a common ancestor. Second, on the assumption that there is evolutionary conservation of many functions across species, comparing communication, cognition and learning in different animal species may also provide insights into the mechanisms that underlie human traits and suggest hypotheses about their evolutionary origins.

Phylogenetic approaches compare similarities and differences in the traits of species related by common descent, i.e., ancestor/descendant relationships. Proceeding on the assumption that human traits evolved from prehuman foundations shared by nonhuman primates, they often focus on comparing primates, particularly the chimpanzee, with humans. These studies examine the relation between processes and mechanisms in humans and nonhuman primates in an attempt to identify and investigate homologies, i.e., characteristics derived from a common ancestor. Given that humans and nonhuman primates shared a common ancestor about 5–7 million years ago, it is plausible that many human traits and their developmental trajectories derive from a common primate heritage.

Ecological comparative approaches study the convergence of traits among unrelated or distantly related species that have faced similar selection pressures as well as the divergence of traits in related species subjected to different selection pressures. These approaches emphasize factors that lead to convergence, i.e., the adaptive evolution of similar traits in phylogenetically distant species. They attempt to identify and investigate analogies or homoplasies, i.e., similar traits that have evolved independently in nonrelated lineages like wings in bats, birds, and insects. Focusing on the ecological variables involved in adaptation, rather than descent, they investigate the characteristics that enable organisms to survive and reproduce in their specific environments. Ecological approaches consider both environmental and social challenges across a wide variety of species, e.g., scarcity or variety of food, predator pressure, collaborative hunting, and cooperative breeding.

Through comparisons they aim to specify the relationships between organisms and the environmental demands that generate adaptations. Since distantly related species subjected to similar selection pressures may be more similar in their traits than closely related species that have faced dissimilar selection pressures, ecological approaches do not limit their research to the great apes.

Indeed, from a comparative perspective there is no reason to confine studies to humans' phylogenetic relatives, even though the rationale for comparing humans and nonhuman primates is clear. In particular, studies of nonprimate species are necessary to disentangle convergent, parallel, and divergent evolutionary processes. Recent studies of nonprimates suggest that several cognitive and behavioural abilities once considered exclusively human are distributed across different species, e.g., category formation in African grey parrots (Pepperberg & Wilcox, 2000), tool manufacture and use by New Caledonian crows (Chappell & Kacelnik, 2002), episodic-like memory in scrub jays (Clayton, Bussey, & Dickinson, 2003), and memorial and selective imitation skills in domestic dogs (Kaminski, Call, & Fischer, 2004; Range, Virányi, & Huber, 2007). Whether these abilities are subserved by similar mechanisms in humans and in nonhuman animals is the subject of ongoing comparative research. Clearly, both phylogenetic and ecological approaches are required to identify empirically those abilities that are uniquely human and place them in an evolutionary framework.

The contributors to this volume take diverse, and often competing, methodological and theoretical approaches to comparative studies. Some take an experimental approach, comparing the specific abilities of primate and/or nonprimate species in controlled laboratory tests, e.g., Burkart (Chapter 6), Caldwell (Chapter 9), and Virányi, Range, and Huber (Chapter 7). In methodologically rigorous experiments these researchers try to identify and distinguish examples of evolutionary homologies and analogies using a variety of experimental techniques and protocols. Some researchers emphasize phylogenetic factors; others follow a more ecologically oriented approach. However, the phylogenetic and ecological approaches are often complementary as Meguerditchian and Vauclair's review of research on nonhuman primate vocalization and gesture (Chapter 3) illustrates.

While studies of laboratory and captive animals permit rigorous experimental control of phylogenetic and ecological variables, they face concerns about the ecological validity of their findings. Field researchers like McGrew (Chapter 10) emphasize the importance of studying free-ranging primates' natural behaviours over a purely experimental approach. Attention to the natural or typical developmental context in which the abilities of humans and nonhuman primates emerge is also a central concern of developmental psychologists like Rakoczy (Chapter 5) and the comparative-developmental psychologists Bard and Leavens (Chapter 4). The use of methods to derive and test hypotheses experimentally as opposed to naturalistic observations or other reconstructive methods is a matter of controversy in numerous

disciplines, as the biolinguistic proposals advanced by Fitch (Chapter 1) and by Wildgen (Chapter 2) document. This controversy is part of a wider debate about the methods, models, and conceptual frameworks appropriate to comparative studies, which the philosopher Brinck (Chapter 8) explores in depth. Comparative findings on the nature of similarities and differences between humans and nonhuman animals also have implications for social and political agendas, e.g., public debates on animal rights or the Great Ape Project. The philosophers Jamieson (Chapter 11) and Kettner (Chapter 12) take up the question of equal rights for humans and great apes and reach opposite conclusions.

Despite agreement on basic evolutionary premises, there are important debates within comparative approaches, e.g., over conceptual and empirical issues or the interpretation and explanation of comparative findings. Of course, disagreements about how to define central concepts like language or culture are not unique to comparative studies, nor are differing interpretations of evolutionary theory, e.g., (neo-)Darwinism, "extended" evolutionary theory (Feldman & Laland, 1996) or considerations from evolutionary developmental biology, "evo-devo" (Carroll, Grenier, & Weatherbee, 2005). There are also empirical issues which are relevant to all behavioural studies, e.g., questions about observational and experimental techniques, the number of subjects or number of times a target ability is manifested. However, in controlled animal studies specific questions about training procedures become crucial.

Moreover, when we consider what can be learned about human capacities from comparative studies, questions about how to interpret and explain findings are of central importance. The relationship between human and nonhuman animal traits that is claimed in a study is crucial and often highly contentious. For example, do the empirical data obtained in comparative studies provide evidence of homologies or merely analogies? Finding criteria for determining behavioural and cognitive homologies is difficult (Rendall & Di Fiore, 2007). It is complicated by the fact that the nonhuman species available for study are our contemporaries, not our ancestors. Consequently, inferred commonalities rest on comparisons with species that branched off from the evolutionary paths that led to the homonid lineage long before modern humans arose. This raises questions about the use of animal models and the extent to which findings can be extrapolated to humans.

There are also questions about how to explain the behavioural and cognitive repertoires manifested by nonhuman animals. Should they be attributed to the simplest mechanisms possible, e.g., associative learning or stimulus enhancement, or does their explanation require attributing more complex forms of social learning like imitation? Furthermore, can explanation proceed by eliminating alternative hypotheses or must a positive account be sought? For example, are variations in chimpanzees' foraging and grooming behaviours to be explained solely by learning mechanisms, by ecological differences, by genetic differences, or perhaps by a combination of all three

(Laland & Janik, 2006)? Which methods should be employed to study which target abilities? Are observations of animals in the wild adequate to study cognitive processes or are experimental studies necessary? The answers directly affect whether and how comparative studies of nonhuman animals can contribute to an understanding of distinctive human traits. Clearly, much information can be gained from both experimental and observational research on how nonhuman animals are similar to humans and how they differ. Nonetheless, the exact nature of the similarities and differences remain controversial as well as the degree to which other animals, especially the great apes, are capable of anything like human language, social cognition, or culture.

Part I, "Language", of this volume is concerned with the evolutionary origins and development of language and speech. The discontinuity between language and other animal communication systems poses a problem for evolutionary accounts of the origins and development of the human capacity for language and speech. Placing human language in an evolutionary framework is difficult, especially from a comparative perspective, because there are no clear homologies to language in animal communication. Nevertheless, no one doubts that the human capacity to acquire and use language is biologically based. Human children acquire their native language without much instruction, whereas other animals do not fully acquire language despite extensive instruction. Researchers agree that a species-specific biological capacity for language exists, independently of whether they regard language as a system of communication, which might be subject to social selection pressures, or as a complex conceptual system for mental representation and thought. The contentious issue is whether the development of language and speech is continuous with the communicative capacities of other animals or whether it reflects a discontinuity.

Did the capacity for language evolve gradually from incremental elaborations and adaptive extensions (homoplasies) of animal communication systems, i.e., through biological adaptations that can be explained in neo-Darwinian terms (Briscoe, 2003; Corballis, 2003; Newmeyer, 1991; Pinker, 2003; Pinker & Bloom, 1990)? Or, did the capacity evolve through some nonadaptationist route (Bickerton, 1995; Gould, 1993; Jenkins, 2000)? For example, could it have emerged through the exaptation of some prelinguistic capacity, i.e., as a by-product of other abilities which were themselves adaptations—from old traits put to new use (Hauser, Chomsky, & Fitch, 2002)? Several researchers propose that the language capacity arose as a by-product of some other adaptation, e.g., a large brain (Chomsky, 1988) or as the result of complex brain structures with mechanisms evolved for motor control (Lieberman, 1984, 2006), of internal systems underlying computation and representation (Bickerton, 1995), or as a result of social cognition and the evolution of human culture (Tomasello, 1995a, 2005a). Others emphasize the differences between language and animal communication, proposing that the language capacity may have evolved in the primate lineage in a single step as the result of a crucial macromutation (Bickerton, 1990). Such saltationist

proposals elicit controversy among evolutionary biologists, but the adaptationist and exaptationist continuity proposals face equally difficult questions concerning operative selection pressures, e.g., what they acted on and the intermediate steps, or questions about which adaptations language was exapted from.

These issues are at the centre of the emerging discipline of biolinguistics, which seeks to relate humans' capacity to acquire and use complex language to biological endowment. Fitch argues that this multidisciplinary field should model itself on the natural sciences and pursue empirically based hypothesis testing, illustrating his proposal with cross-species comparative research on formants, i.e., natural resonant frequencies of air in the vocal tract during vocalizing. In contrast, Wildgen approaches biolinguistics from a semiotic perspective that encompasses linguistics, Paleontological data and models from catastrophe theory. Adopting a comparative biolinguistic perspective, he tackles the problem of reconstructing an evolutionary grammar that specifies intermediate steps from nonhuman animals' capacities to protolanguage and then to the syntactic structure of human language. The primatologists Meguerditchian and Vauclair bring experimental comparative data to bear on the question of language origin. They review comparative research on vocal and gestural communication in nonhuman primates with respect to two leading adaptationist continuity conjectures, the vocal and the gestural origin hypotheses. Arguing that the organization of the vocal and gestural systems sheds light on the question of the origins of language and speech, they conclude that the available behavioural and neurobiological evidence favours the gestural origin hypothesis.

Part II, "Cognition", considers aspects of human and animal cognition and explores whether there is a factor or group of factors that makes the social-cognitive abilities of humans unique. Humans' social and cognitive characteristics differ strikingly from those of other animals, including nonhuman primates—even though humans and great apes share basic forms of primate cognition (Tomasello, 2005a). What makes human social-cognitive abilities so distinctive? One influential answer takes attentional capacities and their development in ontogeny together with a species-specific form of social learning to hold the key (Tomasello, 1999; Tomasello & Rakoczy, 2003; Tomasello, Carpenter, Call, Behne, & Moll, 2005). On this view, a suite of unique human cognitive capacities emerges early in human ontogeny. These include the capacity to jointly share attention to objects and events with others and the capacity to imitate what someone else intends to do, not simply what they do. Thus, in developmental and comparative psychology recent debates about the uniqueness of human cognitive capacities focus on the phenomena of joint attention and social learning and their relation to language acquisition, cultural evolution, and "theory of mind" capacities, i.e., the capacity to understand thought and behaviour in terms of mental states. For example, does joint attention represent a human-specific adaptation that accounts for most of the cognitive differences between humans and

nonhuman primates? Does it provide the basis for developing forms of cultural learning over and above the social learning skills found in apes? Are nonhuman animals, especially the other great apes, capable of selective imitation, or are their social learning skills best explained by simpler processes of observational learning, e.g., stimulus enhancement, social facilitation, imitative copying, emulation regarding the affordances of objects (Tomasello, 1996), or goal-emulation (Huber, 1998; Whiten & Custance, 1996)?

To identify the behavioural and cognitive capacities or developmental trajectories that are specific to humans, it is necessary to compare other animal species with humans, taking the social and physical factors in their respective environments into consideration. Combining developmental and comparative psychological approaches, Bard and Leavens examine how early social-emotional environments and experiences, e.g., rearing context, influence the development of cognitive abilities like joint attention in both human and ape infants. They argue that apes provide valuable models for understanding many developmental features that have been considered uniquely human. In contrast, even though Rakoczy agrees that humans and other primates share a cluster of cognitive abilities, he argues that human children's ability to enter into shared, collective intentionality provides the basis for uniquely human forms of cognition and sociality. Focusing on aspects of human cognition that emerge beyond joint attentional abilities, he investigates the normative roots of human social life and presents experimental data in support of his analysis.

Although Bard and Leavens and Rakoczy reach different conclusions, they highlight the role of social environmental factors in the development of cognitive abilities. However, identifying the relative contributions of phylogeny and ecology to the elaboration of humans and nonhuman animals' behavioural and cognitive abilities is a formidable task. Adopting an ecological approach, Burkart investigates the impact of one social environmental factor, cooperative breeding, on the cognitive performance of marmosets, a New World monkey. Her results suggest that cooperative breeding affects social-cognitive abilities, but that the underlying mechanisms may differ according to primate species. Pursuing a cognitive ethological approach, Virányi et al. investigate the social-cognitive abilities of domestic dogs, which presumably evolved during domestication through a phylogenetic process of enculturation. They document dogs' remarkable attentional and selective imitation abilities and compare the results with similar experiments conducted with human infants and apes. Surveying comparative psychological approaches from a methodological standpoint, Brinck draws attention to unresolved theoretical and conceptual issues and outlines their consequences for the question of human uniqueness. She analyses the array of methods, concepts, and approaches employed in comparative psychology and argues that researchers need to develop a unified theoretical framework to integrate the disparate methodologies and approaches in order to guide ongoing empirical research.

Part III, "Culture", focuses on the question of continuity versus discontinuity with respect to the human capacity for culture. Can the experimental study of social learning and the phylogenetic analysis of living species identify precursors to the human capacity for culture? In particular, is there a continuity in cultural abilities between nonhuman animals and humans? These are central questions in the debates on animal cultures or traditions. Whether nonhuman animals have "culture" or merely exhibit behaviour analogous to human culture depends in part on how the term is defined (Byrne et al., 2004). There is no single, accepted definition of human culture in the humanities and social sciences, although several characteristics have been proposed as defining features, e.g., social transmission, pedagogy, full imitation, cumulative character ("ratchet effect"), shared symbolic content, and collective practices based on beliefs, values, and norms (Boesch, 2003; Boyd & Richerson, 1985, 2005; Galef, 1992; Premack & Hauser, 2005; Tomasello, 2000; Whiten, Horner, & Marshall-Pescini, 2003). If culture is minimally defined as a pattern of behaviours or material features transmitted and maintained by social learning processes, i.e., which are not genetically inherited or elicited by physical features of the environment, then the nature of the cognitive processes of transmission becomes a central issue. For these processes determine whether the candidate abilities exhibited by nonhuman animals represent an analogy of human culture or a homology.

Caldwell makes a case for comparative, experimental approaches to the study of culture and social learning in primates—both human and nonhuman. After discussing how laboratory studies permit researchers to distinguish and analyse components of social learning processes, she presents experimental data on imitation in nonhuman primates. She reviews studies on how and when particular behaviours are sustained by social learning in both nonhuman primate and human groups. Importantly, the existence of distinctive group or population behaviours does not indicate which mechanism accounts for observed differences nor whether the differences are due to social learning, rather than inherited predispositions or factors in the local environment. Thus, it is important to ascertain what kinds of processes support the behavioural or material manifestations in candidate animal cultures, i.e., whether they involve processes of social learning and, if so, which ones, e.g., simple ones like local enhancement and emulation or cognitively complex ones like imitation. Consequently, a crucial question is how to explain behavioural variation within a group or population. Intra- and interpopulation variations in chimpanzees' behavioural repertoires, e.g., tool use to dip ants or to crack nuts and hand-clasp grooming, are leading candidates for animal cultures (McGrew, 1992, 2004). Do such abilities provide clues to the antecedents from which the human capacity for culture has been constructed? Or, is continuity not to be found in culture itself, but rather in the evolution of the cognitive capacities necessary for culture (Galef, 1992)? McGrew takes up the issue of continuity versus discontinuity of human and nonhuman primate culture. He offers 10 suggestions for investigating primate cultures from the

perspective of cultural primatology, a discipline that studies how socially learned behaviours vary among different groups or populations of the same primate species. Drawing on cultural anthropology, archeology, psychology, and zoology, McGrew advocates interpreting "culture" broadly in order to encompass "diversity in continuity". He recommends assuming that humans and nonhumans share traits until proved otherwise to offset pernicious anthropocentric biases. This leads him to address the problem of cultural extinction facing both nonhuman and human primates and the need to preserve a rich variety of cultures.

Do the findings of comparative studies on language, cognition, and culture compel us to alter our relations to the nonhuman great apes? Specifically, are we obligated to extend basic legal rights to chimpanzees, bonobos, gorillas, and orangutans on the basis of empirical findings concerning shared behavioural and cognitive traits? Siding with the initiators of the Great Ape Project, Jamieson discusses the sources of human resistance to accepting the other great apes as moral peers; he argues that humans and nonhuman great apes should be placed on an equal footing. Kettner argues to the contrary that there are no compelling reasons to treat humans and other great apes as moral equals. He contends that being a bearer of human rights derives not from being a member of a biological species, but rather from a species-specific expression of human dignity. On his construal, human dignity and basic human rights rest not on empirical findings, but on the capacity of members of the human species to normally develop a moral stance, which allows them to reciprocally recognize each other as moral status givers; other great apes do not satisfy this criterion.

The significance of comparative studies for understanding human and their capacities is clearly controversial. The chapters of this volume offer an array of answers to the question of human uniqueness, informed by empirical research and critical reflection on the theoretical and methodological paradigms of comparative research. Some explore the biological context of human and animal capacities; others investigate the developmental and/or ecological contexts in which these capacities emerge. Yet others discuss the conclusions to be drawn from comparative studies. This volume invites readers to consider some of the latest developments in multidisciplinary comparative research and to explore for themselves the explanatory prospects and the limits of learning from animals.

ACKNOWLEDGEMENTS

Part I

Language

1   Prolegomena to a science of biolinguistics

W. Tecumseh Fitch

In the first years of the new millennium, the word "biolinguistics" has rather suddenly come into use as an umbrella term for various biological approaches to the study of human language. At least three recent books have "biolinguistics" in the title (Givón, 2002; Jenkins, 2000, 2004), a new journal with that name has just been founded, and the first Laboratory of Biolinguistics (Riken Brain Science Institute, Japan) is producing its first generation of PhD students. Based simply on the divergent contents of the books just mentioned, this nascent field is broad in its interests and incorporates diverse viewpoints, both about what language is and how it should be studied. Despite numerous disagreements, what the scholars embracing this term all have in common is the core belief that the human capacity to acquire and use language is an aspect of human biology, and that it can thus be profitably studied from a biological perspective. While this core assumption of biolinguistics is not a new idea (Chomsky, 1965; Darwin, 1871; Lenneberg, 1967; Lieberman, 1975), it appears to be one whose time has come. The purpose of the current chapter is to survey the potential of this new field, and to highlight some problems that stand in the way of progress.

It is certainly an opportune time for scientists interested in human cognition to adopt a biological perspective, since the tools available to support empirical inquiry into all aspects of biology have suddenly become so powerful. Human brain-imaging techniques are now widely available that allow us to examine neural function noninvasively in normal subjects. After a decade or so of somewhat self-indulgent neophrenology, this field shows signs of maturing into a promising endeavour with important advantages over the patient-based approaches to neurolinguistics that preceded it. These tools will help map the functional circuits underlying language competence, and ultimately help point the way to the underlying computations that are of central interest. Behavioural techniques for investigating language and related cognitive functions, including eye tracking and looking time techniques, are unveiling a complex cognitive world in infants and nonverbal animals that stands in sharp contrast to their limited communicative ability. These accumulating results belie the belief that language is a prerequisite for any form of complex conceptual processing. Finally, and perhaps most

profoundly, the revolution in molecular genetics has produced genome sequences of humans, chimpanzees, dogs, and many other species, and gene sequences of humans turn out to be nearly identical in many cases with homologous genes in chimps, mice, flies, and even yeast. We can now both observe and control gene expression in animal models, and the new results from developmental molecular genetics necessitate profound changes in traditional conceptions of "innateness".

These and other new techniques are generating a flood of empirical data relevant to age-old questions about the development and evolution of language and the mind, data that often demand fundamental changes in our way of thinking about these problems. More than ever before, the biological approach to language has much to offer the linguist, psychologist, anthropologist, and philosopher. Problems that once seemed insuperable, such as interactions between ontogeny, cultural "evolution", and phylogeny, are slowly yielding to concerted theoretical and empirical effort (Deacon, 1997; Kirby, Dowman, & Griffiths, 2007; Kirby, Smith, & Brighton, 2004; Steels, 1999; Tomasello, 2001). But there is trouble in this potential interdisciplinary paradise, and despite considerable grounds for optimism, it is by no means certain that the new biolinguistic approach will be as successful and productive as it deserves to be. The problems facing a future science of biolinguistics come in two flavours. The first, and the less challenging intellectually, are essentially sociological problems concerning terminology, disciplinary turf wars, and struggles for dominance. A reliance on oversimplified models and outmoded distinctions is another important sociological impediment to progress. Although these problems are easily diagnosed, they may be difficult to solve. Fortunately, some of the more deeply entrenched and recalcitrant disciplinary divides and outmoded approaches seem to be breaking down, and I am optimistic that the next generation of young biolinguists, for whom disciplinary boundaries are more fluid, will eventually leave many of these sociological problems behind.

The second class of problems involve far more profound theoretical difficulties, and constitute some of the most serious intellectual challenges of our time, or indeed that science has ever faced. It is on these difficulties that I focus in this chapter. I see three broad areas of conceptual challenge, each of them related to the others. All three demand fundamental theoretical and empirical progress before we can hope to understand the biological basis for language. The first challenge is neuroscientific: Despite huge progress, at a basic level, we still do not understand how brains generate minds. This is as true of a dog's brain as for a human's, and it is true of very basic aspects of cognition, such as vision and motor control, along with language. The most fundamental neurolinguistic questions concern the basic computations underlying language use, and their specific neural basis. Current attempts to address this question remain on a shaky theoretical footing. The second challenge concerns genes and development: How do genes control the development of a single-celled zygote into the trillions of integrated cells comprising

a complex behaving organism? Again, great progress has been made, and the new epigenetic paradigm allows us to reject long-reigning models of the genome as blueprint. However, the complex and circular nature of epigenesis, and the resultant causal indirectness of development, still pose serious conceptual challenges. Although we now understand in some detail how physical structures like the vertebrate limb develop, the principles underlying brain development and evolution remain only dimly understood.

Finally, while the neurocomputational and developmental difficulties are basically biological, and apply to *any* aspect of cognition, the last and most profound difficulty concerns language more specifically. This suite of problems concerns questions of meaning. Put simply, we have a good theory of information (Shannon information theory), but we lack anything even approaching a good theory of meaning (what I intend with this information/meaning distinction will become clear below). Problems of reference, relevance and context-dependent interpretation remain central unresolved issues in the philosophy of mind. The first two problems have matured to a stage where they appear to be accepted as problems of the empirical natural sciences, but these last problems remain in the philosophical category (we don't even know how to devise experiments to help sort the issues out). Although these unsolved semiotic challenges pose problems for any aspect of cognition, e.g., what is it that happens when an organism interprets some stimulus as "meaningful", they become particularly acute when discussing language, which is that aspect of cognition centrally concerned with meaning.

Recent reviews of new approaches and data in biolinguistics are already available (Fitch, 2005b; Johansson, 2005). Therefore, my goal here will rather be to outline and clarify the problems facing the field. As one interested in seeing this field grow and flower, I intend my critical comments to be constructive. I have been working in "biolinguistics" (without knowing it) for the last 20 years, since my decision as a young marine biologist to refocus my efforts on the evolution of language (Fitch, 1994; Fitch, 2000b, 2002b, 2005b). Although I remain optimistic, I have become acutely aware of the difficulties facing the field, in part because successes in various areas have brought the remaining problems into sharper focus. Through my involvement in a recent interdisciplinary foray in biolinguistics (Hauser et al., 2002) and the rhetorically charged debate that followed (Fitch, Hauser, & Chomsky, 2005; Pinker & Jackendoff, 2005), I have also developed a healthy, if depressing, awareness of the sociological problems that await attempts at interdisciplinary bridge building.

In this chapter I will briefly discuss the sociological problems and disciplinary strife that arise from choices in terminology and differing conceptions of "language". These pose important but soluble problems for those with a *bona fide* interest in solutions and will not be my core focus here. I will then outline and clarify some of the deeper intellectual challenges facing biolinguistics, discussing why many currently popular models and metaphors for understanding genes, brain, and language need to be abandoned if we hope

to make substantial progress. In some cases I will also try, tentatively, to sketch approaches to the problem that appear to me to offer promise. But I will be satisfied if the reader, accepting my critique of the "state of the art", rejects my proposals for remediation. Each problem alone is extremely difficult and, combined, as they must be in biolinguistics, even guessing at plausible answers is difficult. Thus, as with any prolegomenon, my focus here is making the problems sharp and clear, rather than offering solutions.

SOCIOLOGICAL CHALLENGES: DISCIPLINARY DISCORD AND TERMINOLOGICAL DEBATE

> The chance that the key ideas of any professional scholar's work are pure nonsense is small; much greater the chance that a devastating refutation is based on a superficial reading or even a distorted one, subconsciously twisted by a desire to refute.
>
> (Langer, 1962, p. ix)

This wise insight accurately diagnoses much contemporary "debate" in biolinguistics, particularly concerning the evolution of language. I know of no other field where scholars seem so ready to champion their own pet hypothesis uncritically, while rejecting those of others as absurd or ludicrous. I confess to finding some of the proposals in the literature uncompelling or even ridiculous on first reading, e.g., Calvin's "throwing Madonna" hypothesis (Calvin, 1983), or the "aquatic ape" hypothesis (Morgan, 1997), but further reading and thought have convinced me that some valuable insights, and probably germs of truth, are to be found in such ideas—for one willing to put in the work of understanding them. Unfortunately, such willingness is too often in short supply, and debate in the biology and evolution of language frequently reduces to either misrepresentation (dismissals based on straw-man caricatures) or arid terminological debates (I dislike the term X for some trait and propose term Y for the same thing). Often the two are combined. This syndrome is particularly true of criticisms of Noam Chomsky, whose ideas so many scholars apparently love to hate. In my opinion, once placed in context and properly understood, most of Chomsky's scattered statements about both language evolution and its biological bases either are rather uncontroversial statements that any modern biologist studying (say) limb development would accept as a matter of course, e.g., that there must be various biological constraints upon the development of the language system, or present unpopular alternative hypotheses that deserve more careful consideration, e.g., language as a tool for thought rather than communication. Outside of his technical linguistics work, Chomsky's main contribution to biolinguistics is his long championing a scientific approach to language as a *biological* phenomenon (Chomsky, 2005). One will search in vain in Chomsky's own writings for the naïve conceptions of Universal Grammar for

which he is so often mistakenly pilloried—one reason his critics typically quote his few scattered statements out of context, if they quote them at all.

My purpose in this chapter is neither to champion nor attack Chomsky's conception of language (for this see Jackendoff, 2002; Jenkins, 2000; Lieberman, 2000)—but rather to argue that such discussions too often miss or leave unmentioned deeper commonalities of viewpoint and approach shared by most contemporary theorists interested in the biology of language. In the next sections I will try to look past the terminology at some uncontroversial facts about the biology of language, briefly discussing the terminological controversies they have driven. My purpose is to shed the rhetoric and move into the conceptual heart of biolinguistics. This will set the stage for the main part of the chapter, where I discuss the core outstanding conceptual difficulties in detail.

"The human capacity to acquire language": The core explanandum

The central research topic in biolinguistics is a characterization and explanation of the human capacity to acquire and use language. That this is an aspect of human *biology* is made clear by the everyday fact that any normal child raised in a human household will quickly, and apparently effortlessly, acquire the language(s) of its family and community, while no nonhuman animal will do the same. The pet dog or cat may learn quite a bit about the social and practical aspects of life in a human household, and often to recognize a few dozen spoken words of the local language, but its abilities to *express* its own thoughts *using* this language are little different from those of a potted plant in the living room. Perhaps more surprisingly, a chimpanzee raised in a human home will not spontaneously do much better: Even with long concerted training apes learn to produce only an indistinct handful of spoken words (Hayes, 1952). Although use of the manual/visual modality via sign or symbols helps apes considerably (Gardner & Gardner, 1969; Premack, 1971), the adult ape still cannot progress to anything like the level of a 5-year-old child, and its "linguistic" utterances will be mostly confined to requests for tickles or treats. Without belittling the accomplishments or value of such experiments (cf. Savage-Rumbaugh, 1986; Savage-Rumbaugh et al., 1993), it is important to acknowledge these limitations as well-replicated biological facts.

Clearly, immersion in a linguistic environment is not enough for spoken language to develop in most organisms. There must therefore be something about human children which differentiates them from other species, and this something provides one of our core explananda in biolinguistics. We might gloss this neutrally as "the human capacity to acquire language". In generative linguistics following Chomsky this capacity is traditionally called the "Language Acquisition Device", and a characterization of its properties termed "Universal Grammar", reviving a seventeenth-century term.

Universal Grammar (before Chomsky) simply designated those aspects of human language competence which, because they are shared by all humans and all languages, went unmentioned in traditional grammars (Allan, 2007; Chomsky, 1966). For example, the notion that words exist and have specific meanings does not need to be specified in a grammar of French—it can be taken for granted. But this is precisely the sort of fact that *does* need to be explained by a successful biological approach to language. The original usage of the term made no particular claims about the nature of this competence, e.g., that it was specific to language, or conversely a general aspect of human cognition, nor did Chomsky's revival of the term, which is quite neutral on such questions by my reading. However, both "LAD" and especially "Universal Grammar" arouse suspicion and rejection from scholars who nonetheless accept that such a human-specific biological capacity exists (Lieberman, 1998a; Tomasello, 1999, 2005b). A huge amount of ink has been shed rejecting the term "Universal Grammar", even by people who accept without question that a biologically based capacity to acquire complex language fully is a uniquely powerful birthright of any normal human, but no known animal. The substantive debate concerns not the *existence* of such a human capacity for language acquisition, which is abundantly clear regardless of terminology, but rather its nature, e.g., the degree to which it is specific to humans, or to language.

There remains, today, no widely accepted term for this central aspect of human biology, despite the consensus about its existence. A recent attempt to break the resulting terminological logjam by introducing two new terms—the faculty of language in broad and narrow senses (FLB and FLN; Hauser et al., 2002)—unfortunately elicited similar reactions (Pinker & Jackendoff, 2005), although FLB was specifically and explicitly intended to capture a much broader and more inclusive conception of the language capacity than the one connoted by LAD or UG. FLN was intended to have a considerably narrower scope, perhaps even denoting an empty set, but has been read simply as "language" by some and "UG" by others. The term "language instinct", popularized in Pinker (1994) has been rejected equally vehemently (e.g., Tomasello, 1995a). Frankly, it is unclear to me whether any acronym or shorthand version of the "human capacity to acquire language" will escape a similar rhetorical assassination. Perhaps the field of biolinguistics will have to do without any such term for the time being (although I would personally vote for "language acquisition capacity" as a relatively neutral designation).

"Innate knowledge"

A similar terminological morass surrounds the term "innate", and particularly the concept of "innate knowledge", although the problems here are at least partly substantive rather than terminological. The deep conceptual problem ultimately stems from the complexity of epigenesis, the complex interaction between developmental programmes and the internal and external

environment of the developing organism (cf. later). But the terminological problem hinges on what we are prepared (or inclined) to call "knowledge". Knowledge is prototypically a representational state of adult minds, implemented somehow in their brains. We know enough about neuroscience to say that this implementation will involve the morphology of individual neurons, their connections with other neurons, and the computational activities these neural circuits engage in. From this perspective, it would be odd to ascribe "knowledge" to genes, or to the just-fertilized egg. But what about the newborn infant's "knowledge" of language? Here we are on uncertain ground, for the child is certainly born with a brain, equipped with proclivities to attend preferentially to certain things (like human voices) and not others (like dog barks or engine noises). Even at birth the newborn already expresses preferences for its own mother's voice, or her native language, or a lullaby she sang while the child was still *in utero* (DeCasper & Fifer, 1980; Hepper, 1991; Mehler et al., 1988; Mills & Melhuish, 1974; Spence & Freeman, 1996)— implying that the foetal environment has already shaped this newborn brain. This constitutes, perhaps, a kind of knowledge. In addition to such rapidly acquired proclivities, the child manifests constraints on the type of regularities it extracts from linguistic input, and these constraints have been argued by many authors to be important or even necessary components of the child's capacity to acquire language. Do such proclivities and constraints constitute "knowledge"?

"An instinct to learn"

Light can be shed on this question by examining the analogous but better-understood situation in birdsong learning, where an elegant and insightful model of a biologically based cultural capacity has been developed by Peter Marler. Most songbirds (nearly half of roughly 9000 bird species) learn their song; a young bird must hear exemplars of the song of its species in order to produce a normal song (Catchpole & Slater, 1995; Marler & Slabbekoorn, 2004). Birds raised in an aviary with other species, but without access to conspecific song, will sing either a completely abnormal song, or (in some cases) will learn the song of another species. Crucially, most birds do not simply mimic the song of adults exactly. In many species, individuals create new, novel songs that are built upon but not identical to the songs they heard as nestlings. This creative aspect of birdsong ensures that each generation hears slightly different songs from those of the previous generation. This process of song transmission across generations, with slight novelties introduced by creativity and/or erroneous copying, leads to "dialects" of birdsong. Birds in different regions sing quite different learned songs. But just as a human child of Chinese descent can learn perfect English, a young bird exposed to a different dialect than that of its parents will master the new conspecific dialect.

Equally crucially, young birds exposed to the song of many different

species will unerringly hone in on the song of their own species. A songbird appears to be born with a proclivity for the song "style" of its own species, to which it will attend preferentially. So the bird's propensity to learn is constrained in certain ways; it is not simply a "general purpose" system that will learn anything it hears. These facts have forced students of birdsong to progress beyond simple-minded nature/nurture dichotomies. Marler's model of birdsong acquisition instead integrates both biological and "cultural" factors, which are inextricably intertwined in an "instinct to learn" (Marler, 1991). Songbirds, like human children, are born with a readiness to master their species-specific communication system, but they are not born knowing this system. Part of this biologically given readiness is a proclivity to attend to certain types of auditory stimuli (conspecific voices and songs) and not others (dog barking, machine noises, etc.). Constraints exist on what can and cannot be learned; there are limits on the sorts of artificial birdsongs a youngster can absorb. These facts show clear parallels with the facts of human language acquisition, and a model of the human cultural capacity as an "instinct to learn" is an important improvement over currently popular metaphors. This conceptual model has recently been advanced explicitly to model the acquisition of human language (Doupe & Kuhl, 1999; Marler, 2000; Okanoya, 2002).

Returning, thus equipped, to the term "innate knowledge", it seems to me misleading to refer to the constraints on the fledgling bird's song acquisition system as "knowledge". These constraints (whatever they might be) are not themselves knowledge but instead influence the knowledge the bird will someday possess. I would make the same terminological caveat, *mutatis mutandis*, about human language acquisition. However, many scholars would be perfectly willing to term such innate constraints "knowledge". I am happy to accommodate them, so long as the distinctions are kept clear between behaviours that are truly innate, e.g., the acoustic structure of human laughter or cry, and the inborn link between these sounds and pleasure or pain, and those, like speech sounds or birdsongs, for which an innate basis for acquisition exists, but where the behaviours themselves depend on structured environmental input to be acquired and expressed. This distinction illustrates why the term "language instinct" is misleading. The prototypical cases of instinctual behaviours, such as mammalian crying or suckling, a chick's escape from its shell, or a fly's grooming, really are genetically coded behaviours, fully functional at birth. "Instinct" properly characterizes the child's *acquisition system*, but not the knowledge that system will eventually acquire. We are born with a language acquisition "instinct" but not language *per se*. Again, the terminology is unimportant, but the underlying principle is crucial. What, precisely, is the nature of the capabilities, biases, proclivities, and constraints that the human child brings to the problem of language acquisition?

Beyond disciplinary discord

> Whenever people vehemently reject a proposition, they do so not because
> it simply does not recommend itself, but because it *does*, and yet its
> acceptance threatens to hamper their thinking in some important way.
>
> (Langer, 1942, p. 238)

The current literature on the biology of language reveals a somewhat depressing disciplinary landscape. Despite agreement about the central interest of the questions and core explananda, and the promise of the diverse approaches and perspectives represented, members of competing factions too rarely cite each other or interact constructively. Theoretical discussions are often dominated by rhetorical battles and ideological or terminological debate rather than constructive attempts to make tangible progress. Much of the criticism that currently divides the relevant fields boils down to "My opponent says we should look to *x* for answers, but I believe we should look to *y* instead". In my view, both *x* and *y* are probably important, and biolinguistics will be far better off if individual researchers restrain themselves to those topics and points they believe are important, and refrain from attacking others who pay too little attention to those topics. There is little to be gained from such attacks, and if my experience is any guide, much to be lost.

One can only hope that, whatever else happens, biolinguistics will shed the unproductive rhetoric of its parent disciplines. In addition to the stunning progress in contemporary biology, the grounds for optimism within linguistics include increasing convergence in widely separated theoretical approaches to syntax (e.g., minimalism, tree adjoining grammar, construction grammar, functionalist approaches), towards heavily lexicalized theories of language, with a few basic and powerful operations, e.g., merge or unify (see Joshi, Vijay-Shanker, & Weir, 1991; Stabler, 2004). Specialists in neighbouring fields like neurolinguistics prove willing to take insights from generative linguistics and test them empirically (Arbib, 2005; Caplan, 1987; Friederici, Steinhauer, & Pfeifer, 2002; Hagoort, 2005b), and biolinguistics as a whole will do well to follow this path. Interest in biological approaches to language seems to be growing rapidly in all disciplines, so those established scholars prepared to indulge in self-destructive turf wars should be equally prepared to watch the incoming neuroscientists and biologists take over the field.

BEYOND EVOLUTIONARIOS: TESTING BIOLINGUISTIC HYPOTHESES

The appropriate models for biolinguistics come from the natural sciences, such as physics in the early twentieth century, and cellular and molecular biology or neuroscience today. Theorists in these fields consider the issues,

define their terms, and propose hypotheses that generate testable predictions. Experimentalists implement empirical research programmes to test the predictions, based on widely accepted notions of good experimental design, e.g., controls for alternative hypotheses, and inferential statistics. The historical success of this "normal science" approach hardly needs emphasizing. Our modern lifestyle from computers and mobile phones to agriculture and medicine relies upon it, and the future thus holds, if anything, an acceleration of progress in understanding the physical and biological world.

There is no reason that theorists and experimentalists should be different individuals, and I think at the present state of play most biolinguists need thorough familiarity with both theory and experiment. This is especially true for evolutionary questions, since generating *testable* predictions is far more difficult than coming up with untestable evolutionary scenarios. "Evolutionarios" are entertaining but typically offer experimentalists little to work with. Despite the dearth of testable hypotheses, and surfeit of evolutionarios in current discussions, the situation is remediable. The onus is on theory-makers to generate clear definitions of terms and hypotheses and practically testable hypotheses. Furthermore, progress will be aided by comparing and contrasting multiple hypotheses, not simply rejecting implausible null hypotheses in favour of single pet hypotheses. Ultimately, as for physics, what biolinguistics needs most are creative empirical tests of hypotheses.

Since Darwin, evolutionary biologists have been testing functional and phylogenetic hypotheses quite successfully, despite our lack of time machines, using the comparative method. Although Language, writ large, is unique to our species, many (probably most) of the mechanisms involved in language have analogues or homologues in other animals (Fitch, 2005b; Hauser et al., 2002), and their comparative study thus offers biolinguistics crucial insights. Furthermore, new genetic techniques make it possible to roughly date the origins of mutations (e.g., Enard et al., 2002). Thus, a combination of a broad comparative approach, molecular genetic techniques, and creative examination of individual differences among humans offers many ways to test evolutionary hypotheses. For a compressed example, consider two venerable hypotheses about the origins of human speech.

Human speech: An example of biolinguistic hypothesis testing

Scholars have debated for centuries whether the lack of speech in other animals results from peripheral anatomy of the vocal tract (H1), or the nature and structure of the central nervous system (H2). Recognizing that dolphins were mammals with large brains, Aristotle suggested that their lack of speech results from their lack of loose tongues and lips (Aristotle, 350 BC). Similarly, the discovery by Europeans of the (speechless) apes led to renewed consideration of the crucial capacities underlying speech, and anatomist Peter Camper concluded that the lack of speech in orangutans was caused by their large air sacs (Camper, 1779). Both of these ideas are special cases of H1.

Other scholars, like Darwin, considered these arguments, but sided with H2, that central neural factors must be critical (Darwin, 1871).

The descended larynx

As a modern instantiation of H1, consider the descent of the human larynx (Fitch, 2000b). The lowered larynx and tongue root of humans was hypothesized by Philip Lieberman and colleagues (Lieberman, Klatt, & Wilson, 1969) to constitute an adaptation to produce a wider range of speech segments (particularly the point vowels, and the "supervowel" /i/, used in vocal tract normalization). At that time, and for the next 20 years, both the descended larynx and vocal tract normalization were believed to be uniquely human (Lieberman, 1984). In my 1994 PhD thesis (Fitch, 1994) I developed a related hypothesis, based mainly on principles from physics and physiology, that human formant perception might build upon a capacity for size estimation predating speech, providing a preadaptation for the use of formants in speech (H3). This hypothesis required formants to be tied to body size, and clearly predicted that formant perception, and its use in size estimation, would be widely present in other animals. Thus, it was based on a number of testable assumptions and made numerous testable predictions, and in the last 15 years my colleagues and I have been busy investigating them. For example:

H3.1   Formants provide a reliable cue to vocalizer body size:
   a   Body size and vocal tract length should be correlated: YES (macaques, humans, deer, mammals in general (Fitch, 1997; Fitch, 2000a; Fitch & Giedd, 1999; Reby & McComb, 2003)); and
   b   Body size and formants should be correlated: YES (macaques, humans, deer, baboons (Fitch, 1997; Reby & McComb, 2003; Rendall, 2005).

H3.2   If perceivers use formants in their own species' vocalizations to judge size:
   a   Many animals should perceive formants: YES: cranes, macaques, deer, humans (Fitch & Fritz, 2006; Fitch & Kelley, 2000; Reby et al., 2005; Sommers, Moody, Prosen, & Stebbins, 1992); and
   b   Subjects should use formants as a cue to body size: YES: humans, deer, macaques (Fitch, 1994; Ghazanfar et al., 2007; Reby et al., 2005; Smith, Patterson, Turner, Kawahara, & Irino, 2005).

H3.3   Selection to exaggerate acoustic cues to body size leads to vocal tract elongation, achieved via:
   a   Lip protrusion (Fitch, 1994); tracheal elongation (Fitch, 1999);
   b   Nasal elongation to exaggerate size (not yet tested);

c   A descended larynx (which should thus exist in nonhuman species): YES: deer, big cats, etc. (Fitch & Reby, 2001; Frey & Riede, 2003; Weissengruber, Forstenpointner, Peters, Kübber-Heiss, & Fitch, 2002); and

d   Secondary descent of the larynx in humans should occur at puberty and only in males: YES (Fitch & Giedd, 1999; Lieberman & McCarthy, 1999; Lieberman, McCarthy, Hiiemae, & Palmer, 2001).

Most of these studies were directly spurred by specific theoretical questions about the evolution of speech. Besides demonstrating that the descended larynx is not uniquely human, and suggesting that both formant perception and vocal tract normalization build upon primitive mammalian auditory mechanisms, these data revealed that formant signals are an important component of vertebrate communication, are used to judge size, and that these ancient shared uses are still operative in modern humans. They provide abundant evidence consistent with H3, the preadaptive hypothesis of Fitch (1994), which thus becomes a serious contender as the original adaptive force driving the descended larynx in our species. Improved speech is no longer the only plausible evolutionary explanation for laryngeal descent, as previously assumed (Lieberman, 1984).

Into the brain

Equally importantly, these and other recent data on vocal production in mammals demonstrate that the vocal tract is a highly flexible, reconfigurable system: Any mammal can lower its larynx dynamically (Fitch, 2000c). Such data offer strong evidence against H1 in its modern form. Furthermore, vocal capabilities cannot be reliably judged based on post-mortem anatomy (or fossils). Although our vocal tract certainly influences the types of sounds we can make, and has presumably been selected in human evolution for its beneficial effects on mechanical control and/or the speed of information transmission (as argued by Lieberman), peripheral anatomy is not a crucial Rubicon that needed to be crossed before humans could evolve spoken language. The descended larynx/tongue root is not the core factor keeping chimpanzees from speaking, and, by process of elimination, that factor must rest in their brains, not their tongues.

This story is of course far from over: Replications remain scarce, and further data are clearly needed. While a plausible case can now be made against H1, and for the preadaptive hypothesis, one might suppose that H3 never could be demonstrated, as the relevant events occurred prehistorically but do not fossilize. Fortunately, this is not true. Comparative molecular biology offers a new and exciting path out of this apparent dead end. If we can uncover the molecular genetic basis for the descended larynx *and* for the complex vocal control underlying speech, we can use the techniques developed

by molecular evolutionists (Enard et al., 2002) to date the selective events that established the corresponding alleles during human evolution. If the selective sweep leading to "descent genes" preceded that leading to "control genes" (in quotes because it is unlikely that the alleles in question function exclusively in these domains), this would be strong evidence against Lieberman's hypothesis that speech preceded (and selected for) the descended larynx (and therefore in favour of the preadaptive alternative). How can we discover such genes?

Conservation and the broad comparative method

A central realization stemming from modern molecular biology is the profound conservation of genetic mechanisms across disparate living organisms: Even traits that have evolved convergently often rely on homologous genetic mechanisms ("deep homology"). This discovery vastly broadens the scope of the comparative method, which has traditionally focused mainly on homology (though see Gould, 1976). The new data pouring in from diverse distantly related species (especially birds and rodents, but including pufferfish, flies, worms, yeast, and slime molds) reveal a stunning consistency in underlying genetic and developmental mechanisms in this diverse assemblage (Carroll et al., 2005). Such underlying conservatism of genetic details was unimaginable two decades ago. Even phenotypic traits that evolved convergently (and are thus homoplastic) often share common developmental and genotypic mechanisms. Therefore, a broad comparative approach that incorporates homoplasy in addition to homology has deep insights to offer. Biologists can avail themselves of a much broader range of species than previously thought, and expect that many of the resulting data will be relevant to human traits (Carroll, 2003; Carroll et al., 2005). Thus, the discovery of mammals with a descended larynx opens the door to genetic and physiological research on the mechanisms underlying this trait. Widespread conservation of developmental mechanisms gives hope (though not certainty) that similar mechanisms may underlie laryngeal descent in humans and in species, like deer, amenable to experimental study.

Similarly and equally important, the existence of other vertebrates with complex vocal learning open the door to an understanding of the mechanisms of vocal control, at both the neural and genetic levels. Although songbirds are by far the best understood group, mammalian vocal learners include cetaceans, seals, bats (Janik & Slater, 1997), and probably elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005). Unfortunately, both birds and tractable cetaceans (e.g., dolphins) have a brain and vocal tract very different from that of humans. In contrast, seals use a normal mammalian brain to control a normal mammalian vocal tract, and thus provide a unique but mostly untapped source of information into the neural and genetic mechanisms underlying complex vocal control (particularly in phocid seals with complex learned "song"; Janik & Slater, 1997; van Parijs, 2003). Currently,

though, most questions one might ask about seal neuroanatomy and vocal production have a simple answer: Nobody knows, because nobody has looked.

In summary, the comparative data indicate that neural factors, rather than peripheral anatomy, provide the core mechanistic basis for human speech capacities. What keeps chimpanzees from talking, but allows some seals to talk (Ralls, Fiorelli, & Gish, 1985) is the configuration of their brains, and not that of their tongues or vocal tracts. But although we have made tangible progress by rejecting the peripheral vocal apparatus as the core factor underlying human speech, this research as yet offers little insight into which aspects of the central nervous system *are* different. This leads us to the first of the "hard problems" facing biolinguistics.

MIND AND BRAIN: THE NEED FOR BRIDGING THEORIES OF NEURAL COMPUTATION

> Trying to understand perception by studying only neurons is like trying to understand bird flight by studying only feathers.
>
> (Marr, 1982, p. 27)

In his book *Vision*, a foundational work in cognitive science, David Marr argued that progress in understanding the visual brain requires research at multiple levels—including the implementational level (neurons and synapses), the algorithmic strategy used to tackle the problem, and the computational-level description of the problem space itself (Marr, 1982). He used Chomsky's goal of formulating a computational model of language (what Chomsky termed a "competence" model), as an exemplar of this approach. While Marr's multilevel approach has been embraced in the computational neuroscience of vision, its application to language remains relatively unarticulated. I think this results at least partially from a failure in the language sciences to fully embrace the insight that progress will require multiple, complementary levels of description, at the computational, algorithmic *and* implementational levels. Most crucially, we need bridging theories that go between levels of description, particularly the computational and algorithmic levels.

Despite a long-running debate between connectionists and symbolists in cognitive science (e.g., the many responses to Fodor & Pylyshyn, 1988), a connectionist model at the implementational or algorithmic level is not necessarily in conflict with a symbolic computational model, but rather a potential complement to it, as clear thinkers in this debate have remained well aware. But accepting the need for multiple levels of description unfortunately doesn't provide a road map for how to formulate models at each level or how to link the levels. For that, lacking a general theory of neural computation, we must currently take a catch-as-catch-can approach, using whatever clues we can find. The problem is particularly sharp given that our most powerful

empirical tools at the neural level, e.g., single-unit recording or experimental gene regulation, are unavailable for the study of language because the species employed lack language, and the techniques cannot generally be applied to humans. At the highest computational level of language, our best guides must still come from behavioural studies, both psycholinguistics and traditional theoretical linguistics, with some help from brain imaging.

Comparative linguistics and typology are important additional elements, since the study of diverse languages can sharpen our focus on the problem by cataloguing the diversity of solutions to it. In a few cases, e.g., metrical phonology and stress systems, linguists have already developed quite sophisticated models that seem capable of encompassing most of the diversity of the world's languages (e.g., Hayes, 1995): Both the required theoretical primitives (such as syllables, stress, feet, and prosodic words) and generalizations (e.g., the "iambic/trochaic law") are relatively clear and uncontroversial. Such aspects of language seem ripe candidates for constructing algorithmic models incorporating psychological data (e.g., Cutler, 1996), which can ultimately be translated to models of implementation. Unfortunately, however, such oases of clarity and agreement are the exception in linguistics. Consideration of the diversity of languages allows one to exclude certain possible theories, e.g., a theory that syntactic structure assignment relies necessarily on word order is falsified by "nonconfigurational" languages like Warlpiri that have free word order (Austin & Bresnan, 1996). However, besides a general agreement on such theoretical primitives as words and sentences, and on the need for structure-dependent rules, there seem precious few specific theoretical claims that are beyond dispute in contemporary syntax or semantics.

Given that research and discussion at the purely computational level have so far failed to converge, perhaps there are lessons to be learned from considering the lower levels of description. A crucial lesson from computational neuroscience has been that progress typically results not from investigations at a single level of description, but by attempts to bridge between levels. It is the intersection of constraints from the different levels that gives us purchase on the problem (Rolls & Deco, 2001). Our theory of colour vision is informed by the understanding that there are three types of cones, and our theory of motion detection by the discovery of separate populations of cells interested in motion and not colour. Similarly, consideration of neural data may help theoretical linguists "cleave nature at the joints" in their attempts to discover robust and useful computational primitives in language. Current brain imaging techniques (fMRI, PET) provide little insight into the computation $\leftrightarrow$ algorithm linking problem. While knowing *where* brain activity increases in some language-related task, e.g., generating an inflected verb, or imitating a spoken word, provides pointers about where to look, it tells us little about what the corresponding computation is. Similarly, systems that provide high temporal resolution (EEG, MEG) can provide indications of *when* certain neural regions are activated, and thus provide better data for testing causal models of language processing. But both still leave open *what*

the actual corresponding computation is: what aspect(s) of the circuit diagram are crucial. Despite the value of brain imaging techniques, we cannot expect them to solve the central problem. For that, we need to distill what we know from linguistic theory into a set of computational primitives, and try to link them with models and specific principles of neural computation.

Unfortunately, appeal to general computational principles may be of limited value. To the extent that vision is best conceptualized as a "bag of tricks", where each aspect of vision (colour, motion, depth perception, etc.) has its own unique solutions, there may be no general conclusions available about computations underlying "vision" in general. The same may be true of "language". However, vision is a far more ancient evolved system than language, so this lesson may not generalize, and certain classes of models seem to pop up consistently. Individual neurons are slow and sloppy, and sometimes die. These basic facts have often led to the evolution of parallel redundant circuits, rather than circuits that seem optimal to electrical engineers. This has led to abstract notions of "natural computation" (Ballard, 1999; Richards, 1988) that hold useful clues for biolinguists building bridges between the algorithmic and computational levels. Thus, although a focus on just the computational level ("competence") remains a necessity in everyday work, consideration of "performance models" (including both algorithmic psychological models and, implementational neural models) should ultimately inform our debates about "natural" theoretical primitives (Fitch, 2005a; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Hagoort, 2005a). Thus, we need linguistic models that are explicit about the computational primitives (structures and operations) they require, and that attempt to define linguistic problems at a fine enough grain so that one can discuss algorithmic and implementational approaches to their solution. We need a list of computations that the linguistic theorist deems indispensable to solve their particular problem, e.g., in phonology, syntax or semantics.

Computational primitives

A nonexhaustive smorgasbord of linguistic computational primitives, based on my reading of the linguistic literature, may help make my point, illustrating the sort of computational structures and operations that any model of language will need to incorporate. While different theorists might give rather different names to them (e.g., Jackendoff, 2002) or object to my overly schematic descriptions, experts can hopefully read between the lines to see what I'm getting at. Alternatively, my list may spur the theoretically inclined reader to generate their own, quite different, list of primitives. This list simply illustrates by example the sort of breakdown needed to begin building bridges between computational theories, and the algorithmic and implementational levels.

1   *Phonology and syntax*.   Trees and related multilevel structures, and structure-building algorithms that concatenate constituents into tree structures, perhaps by forming temporary links among smaller structures stored in long-term memory (the "lexicon"). Evolutionary links with motor control seem likely.

2   *Phonology*.   "Natural classes" of phonemes, such as stops or high vowels. Required because many phonological phenomena apply to specific classes (rather than specific isolated phonemes, or broader class such as vowels). Evolutionarily, natural classes presumably built upon general auditory categorization circuits.

3   *Syntax: Structure-dependent rules*.   Computations that apply to classes of structures (noun phrases or sentences) rather than specific words or broad types such as nouns.

4   *Syntax and semantics: Dependencies*.   We need the equivalent of variables or subscripts that can bind constituents into temporary linkages, such as article agreement, anaphora (binding pronouns to whole noun phrases, in the simplest case), or topic/comment markers in connected discourse.

5   *Semantics: Thematic roles*.   Distinctions like agent versus patient are necessary to distinguish the roles of multiple actors in such propositions as "John likes Mary" versus "Mary likes John". Although English does this mainly with word order, many languages have more flexible ways of marking and expressing this key semantic difference.

6   *Semantics*.   Complex conceptual structures, built up with embedders, conjunctions, and disjunctions with scope. Combining primitive predicates into larger complexes, with possible attribution of an external referent, or truth or falsity, to the whole complex, is a crucial computation in linguistic thought. Despite considerable disagreement about whether this computational capacity is part of syntax, semantics or more general conceptual abilities, there is little disagreement about its basic necessity for both language and other aspects of complex thought.

Tree networks and algorithms over trees

To illustrate how a computational primitive might be fleshed out at the algorithmic and neural levels, consider the first computational primitive: linking trees into larger complexes. First, because tree abstractions appear to be ubiquitous in theoretical models of cognitive phenomena (Simon, 1962), not just language, research in other cognitive domains, e.g., chess playing, music perception, object recognition, or motor control, may offer insights into the nature of linguistic trees. Second, since words have a hierarchical internal structure (Kenstowicz, 1994) and can be thought of as memorized chunks of structure, the processes by which words are learned, stored, and recalled should have much in common with other aspects of long-term memory. Once recalled, such "treelets" must be temporarily combined into larger structures

via some process of binding (either adding a treelet's root to the twig of the larger tree, and thus preserving tree structure topologically, or binding two twigs to create "tree networks"). This process may inherit aspects of the process whereby automatized motor subroutines are combined into temporary motor plans as we execute complex novel actions (Arbib, 2005; Lieberman, 1998b). In the same way that our ongoing plans are sometime interrupted and demand a reconfigured plan, the linguistic tree we have built during an ongoing parse may need to be abandoned and reconfigured, e.g., in garden path sentences. Thus, "performance" theories about how linguistic trees are stored, recalled, and recombined may profit from our preexisting understanding of the neural basis of memory, motor control, and other cognitive domains (as envisioned in Miller & Chomsky, 1963).

At a more abstract level, such implementation-informed theoretical constructs could have important implications for how we formulate our overall theory. For instance, if we conceptualize language as a whole as a system that maps between high-dimensional conceptual structures ("thoughts") onto low-dimensional signal structures (phonetically realized speech or sign streams), it immediately becomes clear that this is an ill-posed problem in the technical sense that there can be no unique solution to the signal→concept expansion problem (due to the greater dimensionality of the target domain), nor perfect solution to the concept→signal compression problem (there being multiple candidate mappings, each omitting something). There can't typically be enough data in the signal to allow perfect reconstruction of the original thought structure. Given this ill-posed problem, what is remarkable is that language works at all for communication and that (in general) we succeed at expressing our thoughts in words, and in reconstructing others' thoughts from their words. The solution demands a massive quantity of shared world knowledge: Far more information is generated by "reading between the lines" than is literally present in the signal. Pragmatic inference using shared world knowledge is a computational necessity.

Evaluating optimality

Syntacticians have long recognized that one aspect of the signal ↔ meaning mapping process is an element of cyclicity in the application of syntactic rules (Miller & Chomsky, 1963). Beyond a certain point of expansion, we become unable to deal with large structures and dangling loose ends: We must "close" or complete old structures if we are to cope with new ones. The first question one can ask is why this effect occurs at all. One likely answer might be that memory limitations ("performance constraints") simply prevent us from what would otherwise be an optimal solution (in much the same way that many theorists agree that memory limitations prevent easy parsing of arbitrarily centre-embedded sentences like "each boy the girl my dog bit kissed was very pleased"). But an alternative answer is that the nature of the concept–signal mapping problem makes cyclicity a computational necessity:

Even an ideal model would include cyclic application of mapping rather than an "all-at-once" compression. Both models are logically plausible, and adjudicating between them would require an idealized model with which to compare actual human performance. Contemporary computational linguistic parsers don't provide such a model, because they assign syntactic structures, not conceptual structures, to strings. Indeed, mapping strings to concepts remains the major unsolved problem in computer language processing. Thus, contemporary linguistics still lacks an "ideal communicator" model comparable to "ideal observer" models in vision, and only once we have such models can we decide whether actual human performance on this task is sadly sub-par, or in fact near optimal.

I focused on the algorithmic ↔ computational bridge in biolinguistics because we clearly have substantial work to do in attempting to build that specific bridge. The good news concerning the other, algorithmic ↔ implementational, bridge is that there is little evidence suggesting that language involves any major discontinuities from other aspects of cognition at low implementational levels. The neocortical circuits involved in language have the same layered arrangement as other nonlanguage circuits, are connected with subcortical systems like thalamus, basal ganglia, and cerebellum in the same ways, and use the same types of cells releasing the same neurotransmitters with the same kinds of action potentials. The developmental processes by which these circuits arise follow the same basic principles as the circuits involved in vision or motor control. Whatever implementational details differentiate language from other cognitive functions, they appear to be only rather subtly different from those underlying other aspects of cognition. Thus we can confidently expect that most aspects of language implementation will be based on more general principles of brain development and function, and that good first-order approximations can be built upon shared principles of neural computation (Ballard, 1999; Rolls & Deco, 2001). We can also expect that such first-try models will uncover some important differences (otherwise, *all* brains, including those of other species, would be able to compute language readily), but these will not rely on wholly new neurophysiology or connectivity. For this reason, I see the **algorithmic specification** of the various components of language, based upon explicitly stated **computational primitives**, as a crucial missing link in our attempts to build the larger bridge between mind and brain. For a similar argument see (Embick & Poeppel, 2005).

GENES, BODIES AND BRAINS: BIOLOGY COMES TO GRIPS WITH EPIGENESIS

A core issue that faces biolinguistics, and biology in general, is development. How can a single cell (the fertilized egg) with two copies of a few gigabytes of DNA, contain within itself the basis for a newborn's body with

100 trillion cells and a brain with a trillion synapses? How can 25,000 genes possibly possess enough information to specify this process? Alternatively, how could the environment *in utero* provide this information? How could evolution have encoded it? Where does all this information come from?

Three *reductios* of naïve models

Let us first dispense with the obvious possible answers in a series of simple arguments, each a *reductio ad absurdum* of the corresponding oversimplistic models. Let us consider the information available for pure nativist or empiricist models more closely. The human brain is estimated to contain roughly 100 billion = 10^{11} cells, each of which has between 100 and 10,000 synapses, leading to at least 10^{14} synapses in the brain. To specify 1 of 10^{11} cells exactly, you need 37 bits. Therefore, to specify simply the connecting cell corresponding to each synapse you would need 37×10^{14} bits (and to specify the synaptic weight you would need at least eight bits per synapse). There are about three billion (3×10^9) base pairs in mammalian genome, so even if the genome was fully dedicated to specifying brain structure (which it is not) and had perfect coding in an information-theoretic sense, we would have a shortfall of at least five orders of magnitude to specify the connections in a human brain: We have 1/10,000th of the DNA we would need to code the detailed wiring of our brains. This "gene shortage" has led scholars like Paul Ehrlich to conclude that little of our behaviour could possibly be innate (Ehrlich, 2002).

Let us therefore similarly consider an exclusive role for the environment. Let us optimistically suppose that we learn something from our environments every second, waking or asleep, of our lives. There are 31 million seconds in a year (3.15×10^7). If we live to 100, that's just 3×10^9 seconds (roughly the number of base pairs in the genome). The first 5 years of life, when most language learning is occurring, contain only 15×10^7 seconds. Even the most fortunate and well-stimulated baby has this paltry number of environmental inputs available to specify 10^{14} synapses. Although we can hope that many synapses are influenced by each environmental input, this doesn't help unless each input event, is very highly structured, carrying a large amount of optimally coded information. This seems optimistic, to say the least.

Finally, for completeness, consider the plight of a different type of nativist: an idealized "evolutionary empiricist" who suggests natural selection alone has programmed behaviour. Vertebrate evolution has occupied about a billion (10^9) years. If we optimistically hypothesize (e.g., Worden, 1995) a few bits of information per generation to accumulate, that's only a few billion bits again (and of course any particularities of the human brain have had far less time—roughly 6×10^6 years—to accumulate). Again a vast information shortfall: this one across evolutionary time.

Are we to conclude from this exercise that development is impossible? Or that the evolution of the brain could not have occurred? No, such basic

considerations force us to reject overly simplistic models, and to conclude that both the naïve nativist (genome as blueprint) and naïve empiricist (environment as instructor) viewpoints are woefully inadequate models. Such considerations quickly lead all serious thinkers on these problems to realize that understanding any aspect of development and evolution requires understanding the *interactions* between DNA and the world beyond the cell nucleus. Despite its tiresome persistence, "nature versus nurture" is a sterile conceptual dead-end, and any promising approach must consider "nature via nurture" in some form or other (Ridley, 2003).

Respect for the cell

An important new insight in our understanding of how genes build bodies and brains is the central role of cell biology in all aspects of development. Crucially, the trillions of cells in our body break down into only 200-odd cell types, and there are only roughly 25 morphologically distinct cell types in the cerebral cortex. What the genome carries is not instructions for individual cells, but instructions for *cell types*. Furthermore, most of the basic behaviour of these cells is shared among all cells in the body (as well as with free-living single celled organisms like an amoeba or yeast), so something like half of our genome deals simply with basic cellular behaviour, and only the *differences* from this "average" cell need to be further specified, e.g., proteins like haemoglobin that are expressed only in blood cells.

Each of the many trillion cells in our body is a semi-independent living thing. Under optimal tissue-culture conditions individual human cells can live for years on their own. This is not surprising when you consider that the first two billion years of evolution took place at the single-cell level. Since single-celled organisms have much shorter generation times than multicellular organisms, most of our ancestors were free-living single-celled organisms. From this history, each of our cells inherits some rather impressive behavioural capabilities. Each cell contains a complete copy of the DNA of the organism of which it is a part; it carries the entire "recipe book" for the entire body. Cells may make epic migrations through the body, following gradients of nutrients and responding to signals left behind by earlier pioneers, and each must eventually find a home and a job in order to survive. Individual cells are highly responsive and adaptable, and can deal successfully with evolutionarily novel circumstances, e.g., finding themselves in a damaged or mutant limb.

Once we recognize cells as active, adaptive, information-processing entities, we see that they form a crucial intervening level of explanation between the genetic and whole-organism levels. The apparent paradox of genetic and environmental information dissolves. Sewell Wright already recognized this in 1931 (Wright, 1931), but the technical details have only recently become clear. From a genetic viewpoint, much of the overall complexity of organisms arises through local interactions between cells and their immediate organism-internal environments. The genome doesn't need to specify the shape of a

human hand or a bat's wing, but simply must constrain the overall pattern of development of a mammalian limb, in a sense "sculpting" a preexisting developmental archetype rather than building an iconic "blueprint" of the final structure (Goodwin & Trainor, 1983). As often correctly emphasized, the genome is nothing like a blueprint and is more like a recipe. Like any recipe, it leaves a lot of detail unspecified, and up to individual cells to "decide" based on their particular history and circumstances. From an evolutionary viewpoint, there is no need for natural selection to perform a detailed and complete hill-climbing process through a complex, mostly non-adaptive morphogenetic space. It can let robust developmental processes do much of the work. Natural selection simply "chooses" among the various relatively worse or better-formed, but still functional, options that result from development. This perspective on cells as prime movers in development and evolution is nicely described, with many examples, in Kirschner and Gerhart (2005).

Epigenesis

Thus, in a way we are finally beginning to understand, recipes for building bodies are constrained both by the information in our genomes and the separately inherited cellular machinery acting on this information. Equally, development is constrained and informed by the environment and has been shaped by evolution to respond robustly to it. Despite the apparent shortfall of information in any one of the relevant domains, the reality of epigenesis —the close interaction between information in the developmental "programme" and information stored in the environment—is that such interaction is fully adequate to specify bodies (and brains as special cases). Environmental stimulation, and even social interactions, turn genes on and off, and development occurs via successive waves of interactions among cells, and between cells and their local environments within the body (themselves structured by previous such interactions). Crucially, the relevant "environmental information" in epigenetic interaction is mostly the local environment surrounding each cell, and *not* that in organism-external world. This local environment has traditionally been left out of both nativist and empiricist models, but is clearly where the action is in development. Each of the trillion cells in our body or the billion cells in our brain has its own, myopic, local environment which informs its DNA regulation and thus developmental decisions. While this local internal environment is, for the most part, dependent upon past decisions made by neighbouring and predecessor cells, it is also often influenced in important ways by the organism-external environment. This influence is perhaps most marked in the brain (which is the organ most specialized to process organism-external information), but other systems like the immune system have a similarly rich external responsiveness.

Epigenetic, interactive developmental models are nothing new: The concept has been standard in embryology for many years (Waddington, 1957).

Experimental embryologists like Spemann recognized that cells respond to messages generated by other cells, and that this determines their fate later in development. Huge advances in our understanding of the genetic basis of development in the last decades have brought such ideas to fruition, and now the molecular basis of Spemann's "organizer" signal, and many other similar cell–cell signalling systems, is becoming clear (see Gilbert, 2003). The mechanisms by which DNA expression is regulated, both in classic epigenesis via transcription factors (proteins that bind to DNA), and longer term changes (e.g., the new epigenetics of "genetic imprinting" that can span generations) are now becoming clear (Reik, 2007). This progress in turn has led to the construction of new bridges between evolution and development— evolutionary developmental biology or "evo-devo"—which promise to finally close the most crucial remaining gap in our understanding of biology (for authoritative introductions see Carroll, 2005; Carroll et al., 2005). Today's biolinguists can help themselves to some well-developed models of epigenesis and development/evolution interactions, before trying their hand at understanding the epigenesis of language.

Neurons: A very special cell class

This cell-based epigenetic perspective, a central tenet of the evo-devo revolution, is as applicable to the development of brains as to the rest of the body. However, neurons are unusual in a number of ways. The most important is that they are specialized for information processing by networks of neurons, over and above the normal cell–cell interactions that influence all cells. In the case of a neuron in the developing brain, "finding a job" means taking part in a circuit that behaves coherently, and many of the neurons that are born fail to achieve this goal, and undergo programmed cell death as a result. While the primary constraints on a skeletal cell are physical forces (stresses and strains), for a neuron the relevant forces are the complex ebbs and flows of an "information economy" established by myriad surrounding cells (both neurons and glia) as well as quite distant neurons influencing it through their axonal projections. Thus, the local environment of the brain is unusual both in the type of commodity processed (information) and the topology of interactions (including precise long-distance connections, made possible by the unusually elongated neuronal morphology). While there is every reason to believe that insights from the development of limbs or the lung will carry over to the brain, we can also be certain that new principles are involved in brain development and evolution (Striedter, 2004). For further implications of this perspective on the evolution of mind see (Fitch, 2008).

The way forward

The revolution underway in developmental biology has important implications for biolinguistics. Anyone interested in understanding the biological

basis for human language acquisition must be prepared to jettison simplistic debates about nature versus nurture, and unhelpful notions of heritability from old-school genetics ("dyslexia has a heritability of 45%"). Instead we can expect highly complex interactions between cells of different types, and in different brain regions, to provide the link between genetic changes and individual phenotypes. We can expect few if any cellular behaviours or cell signalling molecules that are qualitatively novel, either to our species or to language (Hill & Walsh, 2005), but instead combinations of conserved cell processes building neural circuits that perform qualitatively novel classes of computation (Szathmáry, 2001). We can expect that such circuits, built of "normal" neurons using standard neurotransmitters, will exhibit properties and connections that are "standard" in the mammalian brain (e.g., cortico-thalamic loops), but that these same circuits may show patterns of connectivity that are unusual, and perhaps in some cases unique, to our species or to language itself.

It would be hard to overstate the difficulty discovering such subtle implementational differences poses. Those circuits whose structure is already known in detail, e.g., in the hippocampus or cerebellum, have proved remarkably resistant to abstract computational analysis. Although a variety of simple models of memory or motor control exist, computational neuroscientists have yet to converge on models that are simple enough to understand, yet adequately comprehensive. And these systems are broadly shared with our "model" animal species (mice, rats, monkeys, etc.). Integrating our computational and developmental problems, we can expect that *any* simple developmental model of the key neural computations involved language will be incorrect in its details. Nonetheless, progress will be fastest if we attempt to develop explicit simple models of various language mechanisms, amenable to experimental disproof, and then let the data show us where they are wrong. In the same way that Galileo and Newton achieved huge gains in physics by abstracting away from the existence of friction, we may expect that abstract models of neurolinguistic function and development, based on known aspects of neurophysiology and neural development but tailored to the specific computational needs of language, will offer hope of rapid progress. As Einstein advised, "everything should be as simple as possible, but not simpler", and the data will tell us where we are being too simple.

INFORMATION AND MEANING: THE FINAL FRONTIER

I will end with a brief look at the aspect of language that I think promises to be most difficult to solve: the problem of meaning. Although we have a powerful and well-understood theory of information, we still lack a mathematical theory of meaning, and developing such a theory poses some knotty conceptual and computational problems. Here I attempt only to point out the problems, without offering even sketchy solutions. I think the magnitude of

the problem often (or even typically) goes unnoticed in linguistics, where theorists tend to rely on an already-linguistic conception of semantics (a "language of thought" of some sort) without focusing on the far deeper difficulties for modelling nonlinguistic concepts. The last 30 years of animal cognition research leaves little doubt that nonlinguistic animals *have* complex concepts and can reason with these, and in general can have rich, active mental lives—despite their inability to express their thoughts to others (Griffin, 2001; Hauser, 2000; Hurford, 2007; Vauclair, 1996). These predated language and form the cognitive foundation for word and sentence meanings today. Thus, the problems involved in developing an adequate theory of meaning are very broad, and extend far beyond the confines of language or linguistics. Indeed many of the problems have been recognized most clearly in artificial intelligence and robotics, where attempts to build computers that can execute simple but novel motor acts, or recognize basic referents and thus implement even the roughest approximation to "meaning", have thus far been relative failures. Some of the key missing ingredients of a rich cognitive theory of meaning include a subtheory of context and a theory of relevance (for insightful discussion see Sperber & Wilson, 1986).

Shannon information as a foundation

Claude Shannon's formalization of "information" as a quantifiable mathematical entity was a bold, unifying theoretical move, recognized as revolutionary almost immediately upon its publication (Shannon & Weaver, 1949). Its success in technology would be hard to overstate. This formalization was the basis for all subsequent work on digital representation and communication theory, without which today's digital world would be unthinkable, where virtually all communicated material (text, speech, music, images, video, and other data) is rendered as a pattern of bits. Shannon's paper introduced the very term "bit" and the underlying conceptual framework of the digital revolution. Shannon's "information" was also recognized as deeply interesting theoretically, because its intimate formal connection with the physical concept of entropy offers a link between the inanimate world of particles and probabilities with the biologically critical worlds of information and meaning. However, Shannon and coinventor Norbert Wiener both clearly recognized that the revolution they sparked was only partial, because "information" in this formalization is far from identical with information as normally understood. In particular, Shannon and his popularizer Weaver were both explicit that Shannon information fails to incorporate any notion of the *meaning* of a signal. This limitation leads to some nonintuitive propositions in information theory, e.g., that the "information" in white noise is greater than that in a symphony or speech. Despite Shannon's own clarity on the limitations of "information" in his sense, this caveat has remained largely unheeded on two important fronts. From a practical viewpoint the distinction between meaning and information has become blurred,

e.g., in engineering, and from a theoretical viewpoint Shannon's call for an extension of his concepts into the domain of true, biologically relevant meaning has gone unanswered, e.g., in cognitive science or neuroscience.

Although its incompleteness has periodically led to a call to abandon Shannon information theory entirely (King, 2004), this would be unwise given the manifest success of this theory in all domains to which it has been earnestly applied (both technology and neuroscience), along with the steady improvements in the theory (MacKay, 2003). Thus, I think the goal for an eventual theory of meaning should be to build upon Shannon's formalism, incorporating his theorems and extending them. I suggest that two key desiderata for such an extended theory of information, incorporating meaning, are formalizations of context and of relevance.

Context and relevance—"one man's signal is another man's noise"

The same signal may be meaningful in one context and meaningless, or meaningful but irrelevant, in another. At several levels this context dependence is captured by the phrase quoted in the heading. Meaning must be defined relative to some context: a broad temporal-spatial window of data, both organism-internal and -external, much larger than the signal whose information is to be interpreted. This context provides the data relative to which the meaning of any signal is interpreted. A signal, e.g., white noise, may have a meaning of 0, despite its information-rich high bit rate. This resolves the nonintuitive nature of Shannon information: A signal can have high information and low meaning, or lower information, e.g., speech or music, which are quite redundant, and high meaning. Relevance, a basic quantity in any adequate formal theory of pragmatics (Sperber & Wilson, 1986), depends not just on current external context, but also on an individual's current cognitive state: drives, goals, unanswered questions, hypotheses being processed. Relevance is thus in the eye of the beholder, and demands a formalization of external context *and* goal-directed internal context.

We should in principle be able to define ideal observer ("ideal interpreter") models that can extract all the possible connections between all possible signals for a given world and goal context. The well-known combinatorial explosion that results, poses serious obstacles to using such models to control action, because a set of computations subject to unconstrained combinatorial explosion is of little use in real-time computation of meaning. This is the infamous "frame problem" in artificial intelligence (Ford & Pylyshyn, 1996), and the "solutions" to the frame problem currently on offer in AI all essentially involve a priori limits on the extent of this explosion: all variants of what Simon long ago dubbed "bounded rationality" (Simon, 1957) or of Chomsky's innate biases. However, it is unclear that such bounded models can do justice to the seemingly unfettered connection finding revealed by individual human linguistic creativity, or its social ramifications, as seen both

in culture and science. While discussions of the frame problem in technology have grown less central as various work-arounds have been developed, the central epistemological issue in understanding the mind is not solved, or even obviously confronted, by such "solutions" (see Fodor, 2000, chap. 2). Further, no ideal interpreter model alone can capture the relevance of a signal without an additional specification of goals, problem states, behavioural sequence location, etc.

The future: Comparative cognition meets formal semantics?

Given the problems context-dependent combinatorial explosion causes for contemporary computers and robots, the remarkable fact is that organisms seem to rarely suffer from the frame problem. Indeed, simple motor tasks that seem trivial to us (or to a monkey or a dog)—locomoting around obstacles, negotiating novel paths successfully, or picking up highly-variable objects without breaking them—remain daunting for today's robots. At the level of perception, perceptual "mistakes" like illusions are the exception and not the rule, and we seem quite effortlessly to exclude a huge variety of possible interpretations, to converge reliably on a relatively accurate but extremely flexible model of the world—again a trick that evades today's best machines and algorithms. In computational linguistics, even simple sentences generate hundreds of possible parses—but we humans rarely even consider more than one of them. One thing that seems common to many of these feats is our ability to use context of various sorts to prune away all but the most probable branches of the tree of possibilities. Our ability to evaluate the relevance of various possible interpretations builds on this more basic context-dependence to explore models of the future or possible worlds. Almost all of this computational generation and pruning is unconscious (perhaps necessarily so, as argued in Fitch, 2005a, 2008). Furthermore, most of these processing capabilities must have predated the evolution of language, since effortless incorporation of context in decisions of relevance typifies the behaviour of a dog or chimpanzee as much as a human. Thus, in some sense, the conceptual and neural basis of "meaning" is a more basic problem than, and its solution should be logically prior to, an understanding of semantics in natural language. Thus, unfortunately, a general theory of "meaning" ultimately demands a complete theory of how brains make minds, clearly one of the hardest problems left for science to solve. Ultimately, I believe that new theoretical tools will be necessary to understand meaning in the more general nonlinguistic sense I have been discussing, and that the study and modelling of nonlinguistic animal minds will play a crucial role in such an enterprise. For now, an attack on the problem from multiple (hopefully someday converging) perspectives will be required.

Linguistics, in the guise of formal semantics, potentially has much to offer this enterprise. Contemporary semanticists have developed a rather powerful set of theories and formalisms, with truth-value, possible world, and

model-theoretic semantics among the prominent theoretical approaches, and employing a variety of formalisms based upon propositional and predicate calculus and their extensions (Portner, 2005). Such approaches are unlikely to solve some of the deeper problems of an embodied (organism-dependent) and context-dependent theory of meaning, precisely because they intentionally abstract away from such problems. Nonetheless, the tools provided by formal semantics should play an important role in our final understanding of linguistic semantics by providing rigorous definitions of the sorts of problems that must be solved, e.g., logical entailment or scope of quantifiers. Contemporary semantics appears largely to take for granted the existence of nonlinguistic models of the world, though work on spatial language provides a welcome, if narrowly circumscribed exception (Landau & Gleitman, 1985; Landau & Jackendoff, 1993). But real progress in understanding this extra-linguistic context- and relevance-sensitive domain of basic cognition will require considerably more work in this direction, as Jackendoff has consistently argued (2002). Until a well-developed, mathematically formalized cognitive theory of meaning, including basic reference and context-dependent relevance, is available, any biologically based theory of language will remain incomplete.

CONCLUSIONS

With these prolegomena, I have tried to clarify some core problems that face the new science of biolinguistics. The sociological problems discussed at the outset should be soluble with goodwill, mutual respect, and self-imposed restraint. Future biolinguists will recognize that the core problems facing this field are far too big for any one individual to solve on their own (if only because mastery of all the relevant disciplines is impossible for even the most gifted polymath), and will team up to solve them together. I am thus guardedly optimistic that the fascination of the questions and exciting promise of the new techniques and approaches will sweep away many of these traditional barriers to success.

In contrast, the three problem areas that form the heart of this chapter pose serious scientific challenges. Each is daunting in its own right. When these challenges are combined, it becomes clear that developing a biological understanding of human language is one of, if not the, most difficult problems in all of contemporary science. Although I have tried where possible to indicate possible solutions to at least some aspects of the problems discussed, my primary motivation in this chapter was simply to clarify the problems themselves. I think that all researchers interested in biolinguistics can profit from musing over these difficulties, and trying to make them clear. At the very least, a meditation on the gravity and breadth of these problems can induce a humility about one's attempts at solutions, and perhaps contribute somewhat towards remediation of the sociological problems that plague the field. But

in any case, a clear understanding and statement of unsolved problems is the best spur to their solution.

Some outstanding biolinguistic questions, framed as testable hypotheses

I emphasized earlier that the model for progress in biolinguistics will be empirical testing of theoretical predictions, along the lines of physics or molecular biology. Thus, I end this chapter by taking a dose of my own proposed medicine, recapping one testable hypothesis and presenting six more, spanning the range of the problem spaces discussed. The first hypothesis here is recapped from the Human Speech section earlier, as a reminder of the type of multifaceted research programme that we will need to find answers to *any* of these questions. I imagine key contributions by researchers in disciplines as diverse as field and laboratory ethology, linguistics, developmental biology and psychology, molecular genetics, experimental psychology, computational linguistics, comparative neuroanatomy, sociology, and brain imaging. I will make no attempt to flesh out the theoretical underpinnings of these hypotheses, or to detail the experiments that would be involved in testing them; these are left as an exercise to the reader, as a prolegomenon is best summed up with questions, rather than answers. These questions don't begin to exhaust the list of testable hypotheses in biolinguistics, but I hope they give some sense of the potential interest, breadth, and promise of this nascent field, and illustrate the future need for productive interdisciplinary collaboration.

- *Speech followed laryngeal descent*. If size exaggeration was a preadaptation for speech (Fitch, 2002a), human genes controlling laryngeal descent should have fixated before those involved in complex vocal control (see Human Speech section).
- *Speech entails babbling*. If "closing the loop" between production and perception is a prerequisite for complex vocal learning, all vocal learning species should normally babble (show an early stage of autostimulatory vocal play, e.g., subsong in birds) (Fitch, 2006a, 2006b). Untested species: pinnipeds, cetaceans.
- *Signal imitation*. If vocal and visuomanual imitation both reflect an abstract domain-general capacity for "mimesis" (Donald, 1991), auditory and visual imitation abilities in individual humans should be closely correlated. If they reflect separately evolved mechanisms there should be no such correlation.
- *Syntactic power*. If human sentence-parsing capacities indeed occupy the mildly context sensitive level of the Chomsky hierarchy (Joshi et al., 1991; Stabler, 2004), the additional form of memory involved in processing grammars beyond the finite-state level should have the characteristics of a queue, rather than a stack (Fitch, in press).

- *Language acquisition.*   If human language acquisition is just a special case of a general innate capacity for acquiring culture (Tomasello, 1999), then individual children's progress in acquiring language should be closely correlated, both temporally and across individuals, with their progress in other aspects of socialization and mastery of nonlinguistic culture.
- *Semantics and neuronal arborization.*   If natural language has cognitive access to conceptual mechanisms that are encapsulated and impenetrable in other species (e.g., chimpanzees), populations or subclasses of neurons with broadened dendritic or axonal arbors should quantitatively distinguish our brains from a chimpanzee brain, and these arbors should be widely distributed throughout the brain (not restricted to traditional "language" areas).
- *Plasticity of "critical periods".*   If epigenetic interaction between genes and external environment plays a key role in developing the neural circuits underlying language, "sensitive periods" (Lenneberg, 1967) during which such interactions are possible should be plastic. In particular, some classes of extreme environmental change, e.g., adoption, should be capable of "resetting" the language acquisition system in young enough children, with a concomitant change in gene expression patterns in the child's brain. This will not be true of epigenetic processes dependent only on the early developing organism-internal environment.

One can easily generate more such hypotheses, but if the current chapter helps present and future workers in this new field discover a clear answer to any one of these, I would be very pleased.

2 Sketch of an evolutionary grammar based on comparative biolinguistics

Wolfgang Wildgen

LEARNING FROM ANIMALS? CAN LINGUISTICS CONTRIBUTE TO THE QUESTION?

In any interdisciplinary endeavour that aims to link the comparative ethology of animals with linguistics, a crucial question is which theory of language is to serve as a starting point. The challenge lies in adequately specifying the grammar of human languages in an evolutionary perspective. The contribution of linguistics to such interdisciplinary research has often been inadequate for two reasons. First of all, current linguistic theories are usually based on a longstanding tradition of normative grammar and an analysis of written language—hence the relevance of grammaticality and competence in Chomsky's models. In everyday speech language use is more variable and more context-dependent and changes-in-progress are pervasive. If we compare humans to animals, the dominant informal behaviour of humans should be the starting point for comparisons and not highly formalized behaviours regulated by institutions like schools, academies, etc. Second, linguists have a historical bias towards logical (analytic) descriptions and lack dynamic or self-organizing models. Therefore classificatory devices and hierarchical knowledge trees like phrase structures are emphasized, while the underlying forces, goals, benefits, trends, and changes are neglected. As a consequence, the intrinsic relation of language to holistic action patterns or to multichannel cognition (visual imagination, musical structure) is misrepresented in the standard models. Evolutionary biologists should turn instead to cognitive linguistics (semantics) and to pragmatic and dynamic linguistics (cf. Wildgen, 1994). In an interdisciplinary cooperation between biologists, psychologists, and linguists, one must assume that new models will be necessary that are not just versions of current types of grammars. In the following sections I will sketch the features of a model suitable for cooperative research in evolutionary biology and linguistics.

A PRAGMATIST POINT OF VIEW ON THE EVOLUTION
OF LANGUAGE

From its inception pragmatics has had a strong link to anthropology and evolutionary theory with its central concept of adaptation. But one must distinguish the adaptive processes found in animals, which shape instincts, from the macroprocesses of linguistic adaptation. When Whorf describes the world-view of the Hopi, he can point to a divergence in human cultural adaptation, which resulted from a separation of migration routes giving rise to the Amerindian and the European populations some 40 to 50,000 years ago. On this time scale the relevant adaptations are cultural ones, whereas changes between the *Homo erectus* (*ergaster*) and *Homo sapiens* are based on biological adaptations.

Although a gradual transition from communication in animals to language in humans is evident to the pragmatist, as it was to Darwin, several approaches in theoretical linguistics take the opposite position. Fitch et al. (2005) focus the question of language evolution on an "abstract core of computational operations, central to language and probably unique to humans" (p. 180) and they try to neglect the "myriad component mechanisms" (p. 181), which are not unique to humans. What remains is called FLN: *faculty of language in the narrow sense*. As they remark, FLN "could possibly be empty if empirical findings showed that none of the mechanisms involved are uniquely human or unique to language". For Fitch et al. the best and currently the only candidate for a component of FLN is the "computational capacities of recursion" (p. 204). All explanations that argue for an adaptive origin of this core feature are dismissed; the authors argue that only synchronic adaptation is acceptable as empirical evidence. In consequence, neo-Darwinian evolutionary explanations of human language are considered unscientific, because they are not testable here and now.

As is often the case in recent debates in linguistics, the opposing view also has proponents. Jackendoff and Pinker (2005) argue that recursion is found in the human visual system, too, and thus it is not specific to language, i.e., not part of FLN, which consequently would be empty. Moreover, they reject the "narrow syntax" view of language in the Chomskyan paradigm as scientifically unproductive. Moving beyond the controversies within Chomskyan linguistics, I will adopt a radically different approach, which highlights the *pragmatic* origin of our capacity for language, not the origin of presumably universal formal features, and draw on relevant data from palaeontology, anthropology, genetics, sociolinguistics, neurolinguistics, and descriptive linguistics (cf. for "evolutionary pragmatics", Wildgen, 2007b). Fundamental questions about the origin of humans and human language differ significantly from questions about the correct grammatical account for vowel phonemes, grammatical morphemes, or word order in dialects studied by linguists. The best one can aim for with respect to basic questions like the origin of language is to reduce the huge number of

hypotheses proposed. Hence, a central goal is to overcome the myriad ad hoc narratives that plague discussions on the origin of language.

SOME LEVELS OF THE EMERGENCE OF GRAMMAR AND THE HYPOTHETIC LEVEL OF A "PROTOLANGUAGE"

Despite the impression of coherence conveyed by current grammars, the language capacity does not arise from a single source or a single cause. Briefly, it is not God given, nor the result of some mythical pseudo-Darwinian mutation. Its origins are located at different points in time during the last millions of years and these represent a response to very different ecological (selective) conditions. A stratification that corresponds to this series of causing or channelling conditions and to the consecutive adaptations (in the context of the evolution of the climate, the flora, and the fauna) can be recovered from current linguistic behaviour. Features that evolved earlier have a different place in the cerebral (bodily) architecture and are functionally presupposed by more recent strata. One may postulate the following stratification:

1   *Basic level.*   The most basic cognitive level contains the capacity of efficient locomotion for causal impact on the environment and action. If consciousness is added, one obtains a set of dynamic scenarios that control intentional behaviour and a grasp of causality.[1]
2   *Emergence of productive vocal articulation and auditory perception.*   At this stage powerful perceptual and motor faculties for vocal communication evolve. This capacity was further elaborated with the advent of vocal communication for social comfort and control. The basic principles of phonology may have emerged in this period.
3   *A protolanguage based on a compositionally enriched lexicon.*   The underlying capacity characteristic of this stage is a very systematic exploitation of the affordances of the ambient and changing ecology. This capacity was amplified by profiting from the growth of associative areas in the cortex. It probably evolved continuously in a long period between the migration of *Homo erectus* and the reign of Cro-Magnon man.
4   *The evolution of syntactically and textually complex languages.*   This stage emerges with the mastering of stable valence patterns and the use of verbal art (narratives, rhetoric, song, myth). It allows a canon of myths and other text-based cultural traditions to be established. This level probably emerged with archaic *Homo sapiens* and was fully evolved and functionally exploited in Cro-Magnon populations, which created the first large cultural networks (cf. Wildgen, 2004, chap. 8).

In our search for the human capacity for language, we should respect the evolutionary stratification of the linguistic capacity of humans, which contains the levels of:

1   action/motion perception and planning (dynamic archetypes)
2   phonetic/phonological principles and routines, such as basic feature distinctions, syllable structures, rhythmic and euphonic constraints, i.e., phonetic universals and principles of phonological self-organization
3   universals of lexical fields, polysemy, metaphor, and compositionality principles for words or similar entities
4   syntactic and textual principles for the organization of larger linguistic gestalts.

Since Darwin's theory of evolution the basic idea has been that of a continuous evolution moving by infinitesimal steps. Applied to language, linguistic capacities should derive in a continuous series of steps from communicational habits and intellectual capacities of mammals and animals in general. According to Darwin, the hypothetical "protolanguage" can only be the construct of an intermediate stage which helps to fill the gap between animal communication/cognition and human communication/cognition. Recently Derek Bickerton has made several proposals for understanding *protolanguage*. He characterizes his methodology as follows:

> If there indeed exists a more primitive variety of language alongside fully developed human language, then the task of accounting for the origins of language is made much easier. No longer do we have to hypothesize some gargantuan leap from speechlessness to full language, a leap so vast and abrupt that evolutionary theory would be hard to put to account for it.
>
> (Bickerton, 1990, p. 128)

He uses data from pidgin and creole studies, data in primate and child language acquisition, and Kaspar Hauser cases. I shall instead consider the traces of semiotic activity in hominids and early man down to the emergence of writing systems as data for the reconstruction of intermediate forms of human language. This strategy has two consequences:

- Insofar as the contours of early semiotic capacities can be reconstructed from artifacts and art, one can only infer the semantics (and perhaps the pragmatics) of an earlier language capacity, not its lexicon or syntax.
- As the artifacts pertain to the cognitive level rather than to the level of linguistic expression, the reconstructed semantics must be a type of cognitive semantics.

As the evolutionary process is in principle continuous, the term "protolanguage" designates a zone between the linguistic capacities of early hominids and modern humans. In general, the existing empirical evidence is used to make an informed guess about one possible intermediate stage. In this perspective, an evolutionary grammar must account for the starting point,

i.e., the symbolic capacity of the last common ancestor (LCA) some five to seven million years ago via a hypothetical protolanguage, down to the languages of modern populations currently being investigated.

THE FORMAT OF AN EVOLUTIONARY GRAMMAR[2]

The project of developing an adequate format for "evolutionary grammar" encounters problems similar to those faced by developmental grammars, grammars for linguistic change, diachronic grammars, or models of grammaticalization and grammar-genesis. Labov (1972) tried to adapt his sociolinguistic data to modified versions of a generative grammar, as did Klein and Dittmar (1979). Developmental studies adopted the generative paradigm in its Principles & Parameter version and Bickerton (1990, p. 199ff) reduces eight modules of the Chomskyan model current in 1990 to two modules: phrase structure (X-bar-theory) and verb-argument clusters. These two are then used to distinguish the protolanguage of *Homo erectus* and *neanderthalensis*, which would be structurally limited insofar as neither complex phrases nor verb argument complexes could be mastered. I shall give an alternative formulation of these two features (cf. Bickerton, 1990, pp. 189–197).

Decades of attempts to adapt the theoretical models of grammar to the concerns of interdisciplinary linguistics demonstrate that a system of rules—even one with basic categories, modules, and principles—is not able to map the inherent (and not just parasitic) developmental, historical, and evolutionary character of language. The grammatical tradition of normative grammars, school grammars, and competence grammars falls short of the requirements. In general, models that deal with the dynamics of language are required (cf. Wildgen, 1994). A basic insight of interdisciplinary linguistics from socio- to neurolinguistics is that the semantic and pragmatic aspects of language are the primary focus for any explanatory enterprise in this field.

The semantics of space and time in a protolanguage

One can distinguish two subaspects: processes in space, such as spatial orientation and navigation, and temporal and rhythmical patterns. The representation of space has to do with boundaries in space and perspectives on them. A first perspective is centrifugal. It has its point of origin in the individual and bodily motions and leads to the construct of an *experienced* three-dimensional space: in front of–behind (go), above–below (climb, fall), left–right (grasp with the left hand or the right hand). This space of bodily motion involving feet and arms defines the immediate space where objects may be approached, grasped, and manipulated. The intermediate space depends on man's ecology; it can be housing (the cave, abri) or the village. The distal space contains roughly all possible itineraries, e.g.,

of hunting/gathering. The latter perspective is centripetal, i.e., the individual is seen as the location of effects triggered by external causes. The sky, the horizon (typical points where the sun rises or sets), the favoured direction of winds, or a ridge of mountains may be the external locus of orientation for the individual, which is at the centre of a field of force defined by these boundaries. Many myths and religions refer to this extreme locus of orientation when they interpret the fate of humans as standing under the control of distant (and often invisible) forces, e.g., God–in heaven, the devil–underground.

As soon as space is specifically organized in relation to cognition and social use, it enables a cycle of social "investment". Architecture and the spatial organization of villages (or later towns) are clear examples. The spatial organization produces a type of cyclic structure in which different partial orientation functions cooperate. Figure 2.1 depicts such a cycle.

Specific symbolic media are rooted in each subspace and coevolve with it. Thus the painted Paleolithic cave in the Franco-Cantabric culture is a specification of mythical/ritual space; it is also connected by its illusionist paintings to the ecological space of hunting. The relation is iconic, indexical (in its magical impact), and symbolic (in its abstract signs; cf. Wildgen, 2004, pp. 80–83). The dark painted cave is related to cave openings, abris, and huts where people live. The open space in front of the cave openings or huts is a public space where the production of artifacts and the distribution of shared food occur. This public space is the border to the open field of the chase and harvesting. Human action patterns occur inside a specific space or make a transition from one space to the neighbouring one. In rituals the core of these action patterns is fixed. The coding of action patterns by rituals is a social preparation/presupposition for linguistic rules/grammars.
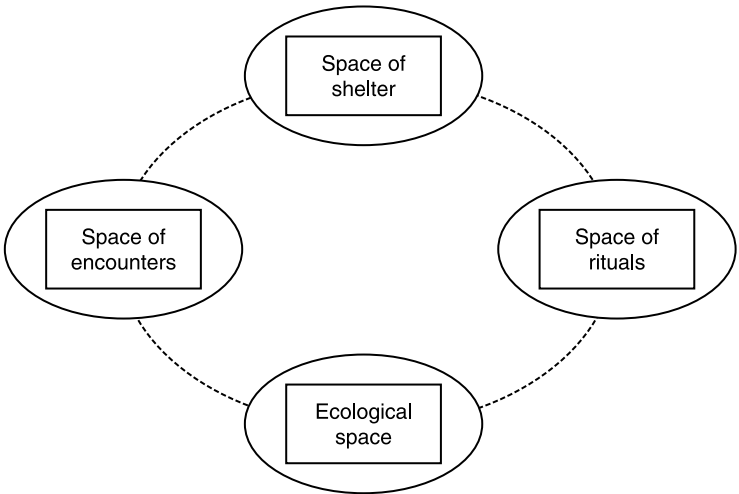
Figure 2.1 Functional subspaces and pathways that are linked to each other.

The cognizance of such schemata for orientation may only be evident in behaviour as it is in many animals; it may be gestural or it may be deictically organized in a phonic language (cf. Levinson, 2001, p. 317ff). For *Homo erectus* the cognizable space seems clear. The inner space is defined by the use of hands and instruments; the proximal space by the choice or construction of dwelling-places to which the group could return. The centripetal organization is involved in long-range excursions and migration. Since the orientation system cannot be genetically coded, it must be learned, adapted to changing contexts, and socially shared. Language is one possible solution to this problem, be it gestural (behavioural) or phonic. As humans have chosen the path of phonation, it is plausible that our ancestors began to proceed further in this direction.

The representation of *time* is rooted in the classification of multimodal sensory inputs using specific temporal rhythms (clocks). Pöppel (1994, 1997) proposed two temporal windows for multimodal integration:

- The window of 30 ms. An event becomes an object of (multimodal) perception only after a stability of 30 ms. It can then be classified, labelled, compared, i.e., further processed.
- The window of 3 s. A sequence of events can be understood as a structure. In this window the smaller units (> 30 ms) are correlated as: before–after, cause–effect, etc. This is the point where a notion of structured temporality is born.

A protolanguage must categorize events and actions (by protoverbs) and must discriminate stable entities (by protonouns). The question arises as to whether temporal, dynamic, quantitative, and qualitative *relations* between them can be mastered and if so, to what degree. This question brings us to the two basic delimitations of a protolanguage, as discussed by Bickerton (1990): first *case-frames* or *scenarios of action* (government) and second *phrase structure* (X-bar-structures). I will argue in the next sections that there are intrinsic complexity barriers which could have blocked the further elaboration of a protolanguage over a long evolutionary timespan.

Scenarios of actions and events

The event-schemata derived from catastrophe theory can be employed as a measure of complexity (Wildgen, 1982, 2005). Let us take grasping with the hand as a starting point. The action-concept GRASP involves the body (the hand) and an object and presupposes the perception of stable entities in the 30 ms window. The whole schema should fit into the 3 s window, e.g., in the sentence:

The father **takes** the book (from the table).
agent   **object**   **location**

If we add two or more GRASP scenarios and integrate them spatially and temporally, more complicated scenarios can be generated:

The father **gives**	the book	to his son	(in the living room).
agent	*object*	*patient (goal)*	*location*

The son **hits**	the ball	with his racket	(in the yard).
agent	*patient*	*instrument*	*location*

However, these elaborations are a considerable step beyond the simple (two value) schema of grasping. They require higher cognitive controls and a social demand for such complex habitually occurring scenarios (in Figure 22.2 the label "I" designates an *intermediate* entity, which is either the object transferred or the instrument used; cf. Wildgen, 1994, p. 129.)

Early humans, e.g., *Homo habilis*, already had a hand with the opposition of thumb and fingers, but some features are still linked to climbing as in gorillas and chimpanzees. The *Homo erectus* had a hand that was adapted to strong grasping (cf. Piveteau, 1991, p. 74ff). This was still true of Neanderthals. A shape of the fingers that slightly deviates from the statistical average can even be found in some human populations.

One may distinguish three types of grasping:

- the force grip (e.g., of a branch)
- the precision grip (e.g., of a small tool)[3]
- the refined grip (e.g., of a needle).

These distinctions, which have a long evolutionary history, constitute a kind of manner specification in relation to the GRASP schema. As the distinction between the types of grips shows, more elaboration appears as soon as more precise manipulations on objects and instruments are developed. The fact that a cognitive bivalent schema and a manner component were mastered does not necessarily mean that they could be transformed into phonic signals. One could even argue that the teaching of hand skills does not call for linguistic
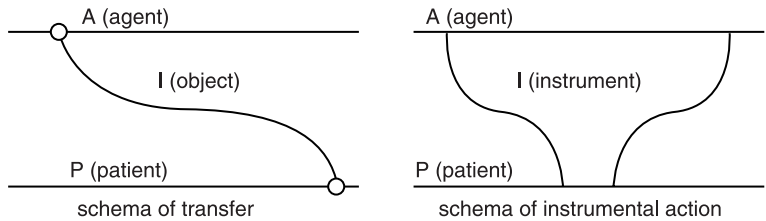
Figure 2.2 Schema of transfer and schema of instrumental action. The catastrophes contained are: A (the agent) emits I (the object) and P (the patient) catches I; in the schema of instrumental action I is the instrument that affects the patient.

instruction. If we assume frequent vocalization, inferred from the evolution of the sublaryngeal tract and a steady increase of memory due to the growth of the brain, it becomes clear that this cognitive schema and subsequent ones are preadaptations for the evolution of verbal phrases or valence patterns in sentences. Thus, in order to verbally represent important and recurrent actions in a protolanguage the cognitive schema of grasping could serve as the basis for iconic/metaphorical transfer to all kinds of manipulations on objects. As soon as instruments are employed, this schema could be iterated.

- The father (A) takes a hand-axe (B) to *move/change/kill* some object (C).
- The father (A) takes a stone/bone (B_1) to *hit/shape* the pebble (B_2) that should later *kill* the animal (C).

In this development a first barrier of complexity appears. While the GRASP schema is dynamically and topologically simple, the composition of such schemata is not simple. One needs a specific topology/geometry to restrict the degrees of freedom for such a composition. Therefore, the GRASP scenario and its bivalent (asymmetric) pattern describe the constitutive plateau of a protolanguage, from which the evolution of a full-fledged language could begin. The evolutionarily old distinction between types of grip and manners of locomotion, related to the dynamics of the legs, is a preadaptation of the manner component in spoken (or gestural) language and could well belong to the basic constituents of a protolanguage.

A set of rather abstract specifications which are often grouped together in pidgin and creole languages can be called the TMA-component (T = Time, M = Mode, A = Aspect). They are the next step that could have "evolved" in a protolanguage on the way to higher level grammars. Gestures or tonal modifications were possibly the precursors of morphemes specifically devised for that purpose. Thus, the order of emergence of grammatical features transcending the GRASP scenario could have been:

1　the elaboration of the manner component
2　the elaboration of the TMA component
3　the elaboration of valence patterns (up to valence 3 or even 4).

One has to assume simpler schemata underlying the GRASP scenario, such as the schema of stable existence. If we apply the 3 ms window, any entity that does not change within this window is a candidate. As the inputs of classification or labelling-reactions are not only spatiotemporal events but also qualities, one can assume a slow increase in quasinominal/adjectival labels as soon as memory capacities grew and corresponding social demands appeared. One could imagine that labels for animals, plants, other people, and artifacts were the first candidates for a growing lexicon. This development is also the natural continuation of classificatory capabilities in other mammals and even in birds and fish.

Cognitively, the manufacturing of stone tools and a fortiori of tools shaped with the help of stone tools goes beyond the GRASP scenario. One hand or one foot must fix the pebble, the other hand grasps the stone or bone that hits the pebble. Finally, the planned chipping off subtracts material from the chosen stone and after several strokes the desired sharp edge of the pebble is produced. This scenario involves two objects, two hands, and a change in the shape of the pebble (the separation of parts from it). This schema contains four symmetric "grasping/emitting" subschemata (simple instrumental action) and one further "emitting" schema. The integration of the shaping by the tool is on a higher level of complexity (it has two force dimensions) and has structural stability only under very specific conditions. In fact, a linguistic description of the action normally requires more than one basic sentence pattern in actual languages. In this sense Paleolithic industries drove the evolution of symbolic tools like language.[4]

The complexity of (nominal) phrases

Bickerton suggested that in order to organize a descriptive (nominal) language one needs three structural layers:

> (a) a generic class, X; (b) the properties peculiar to particular members of that class (large, with a dark red cover, of Mary's) and (c) the specification of the complete individual in terms of abstract relations such as quantity, proximity, familiarity, and so on (a, this, there).
>
> <div align="right">(Bickerton, 1990, p. 195)</div>

His proposal again reflects a position typical of generative grammar (in 1990). In Chomsky (1995) many of the specific features of the Principles & Parameters model are abandoned, because they "appear to be computationally irrelevant" (p. 389). I think that there is no need to follow the traditional X-bar-schema in an "evolutionary grammar". The primary reason is that the function of determiners (a, this, there) differs from other specifiers (attributes), e.g., they rather specify types of deixis or the anchoring of an utterance in context. Their evolution probably followed the evolution of manual and/or visual deixis and later incorporated these devices into the phonic code making them more reliable and less context dependent. This function may be called indexical and exhibits another evolutionary path linked to traces and effective binding between language and nonlinguistic action.

The head (e.g., the noun) and its attribute (e.g., the adjective) share the basic feature (+ nominal) and the problem to be solved is the risk of improperly blending two or more semantic spaces. A semantic space may be conceived of as defined by a set of independent features, which are either polar oppositions or graded scales. Ideally, a semantic space should be homologous to an imagined space, i.e., the hearer/speaker should be able to "flatten" it until it has no more than three dimensions. The imaginative

content of meaning is only accessible under this restriction. A very general notion of mental spaces (without topological restrictions) is employed by Fauconnier (1997). The notion of conceptual integration put forward by Fauconnier and Turner (2002) elaborates this approach, taking up insights from the cognitive theory of metaphor (cf. Wildgen, 2008, for an introduction to cognitive grammar). I suggest that these proposals could be applied to the phenomena discussed in this section.

If every noun or adjective is associated with a place in a semantic space, then the mapping of one place in space A to another in space B is a problem insofar as the spaces are different and may not be easily transformed into a conjunct space A×B. This is possible if A is *father* and B is *old*; in this case *old + father* has a new, well-defined place, insofar as *age* is an implicit feature of humans. It is not the case, if one tries to combine *father* with adjectives like: *narrow, deep*, or *fluid* and *quadratic*. Moreover, if A has *n* dimensions and B has *m*, then A×B may have *n+m* dimensions (if space A is not contained in space B or vice versa) and any increase in dimensionality creates new instabilities; this is a general result of topological dynamics. Another problem is that the mapping of a space A to space B under deformation (insecurity, vagueness, variation) easily produces chaotic results as experiments with video feedback have shown (Wildgen, 1998). Thus Bickerton (1990) dramatically underestimated the problem posed by (iterated) attributes of nouns. On the basis of these considerations, one can specify an *evolutionary barrier* concerning the blending operation necessary for groups with two or more constituents. Hence, the proper hypothesis is that such products of semantic composition were not (or not stably and reliably) accessible to speakers of a protolanguage.

The self-organization of a grammatical system

Pinker and Bloom (1990) think that the central human feature of language is syntax and that an evolutionary theory of language should therefore explain the selection criteria for the syntactic abilities of modern humans. In contrast, Kirby (2000) argues that compositionality (and thus syntax) may emerge if the size of the lexicon, i.e., the meanings associated with linguistic expressions, increases and if individuals learn from utterances. In a computer simulation he shows that after a stage of random invention (and noise) a sudden change occurs, after which: "The number of meanings covered increases dramatically, as does the size of the grammar" (pp. 313–314). A further stable state emerges when the number of meanings increases and the size of the grammar decreases. The resulting grammar is not only compositional, but also "groups all the objects . . . under one syntactic category . . . and all the actions . . . under a second category" (p. 314). Given a certain size of the lexicon and a process of language learning, a syntax can evolve with no Darwinian selection required. In search of further answers one may turn to the mechanics of sign production, i.e., to phonic evolution. MacNeilage (1998) proposed

a mechanism in his "frame/content theory" of the evolution of speech production, which leads to higher order organization in language. Studdert-Kennedy (2000, p. 171) states in his comment on it: "Both short- and long-term phonetic memory were also essential pre-adaptations for syntax. . . . Without a pre-adapted system for storing phonetic structure independently from its meaning, syntax could not have begun to evolve."

The purely syntactic problem of chaining elements of an existent vocabulary therefore does not require a specific endowment or evolutionary processes enabling it. The deeper problem is that of semantic compositionality, because the mapping/blending of spaces with different topologies and accounting for the dynamics inherent in verbs is crucial for sentential units. This is the central problem that early humans had to resolve in order to allow for stable and reliable communication via phrases and sentences. In order to arrive at a level of syntactic behaviour, early humans had to accommodate two major factors:

- They needed the cognitive capacity for a stable solution to semantic compositionality. This is the *cost* of higher order language capacity.
- There had to be a social demand for a compositional level of referentiality in communities of humans. If this demand is satisfied, the *gain* of higher order language capacity becomes apparent.

Rewarding situations probably often arose by chance and the evolving species spontaneously used the "dormant" capacity. With the increase in population density and in networks of supraregional communication and exchange among modern humans such a system very likely became necessary. As soon as it was developed, it established long traditions of language use down to modern times. Since language is deeply rooted in human biological endowment, the turning point in the use of cognition for language must lie before the rise of modern man, i.e., before at least 100 ky BP (thousands of years before the present) and probably even before 200 ky BP. Thus, the central question is not how syntax came about, but what made it rewarding to use the available cognitive potential for syntax. The pay-off could be social or individual, which in turn could lead to higher social competence and thus to social gain.

A cognitive and functional explanation should take the role of language in (silent) thinking as its point of departure. If thinking is a kind of silent speaking learned in early childhood, the complexity of an internalized language could provide advantages for silent deliberation and planning, even if it is not always uttered in social communication. The intellectual advance would indirectly lead to advantages for the community, e.g., having (and listening to) individuals able to act strategically and to plan effectively or to solve other difficult problems. These communities could be selected for their superiority in competitive situations. The role of specialists (technicians, artists, and scientists) is highlighted by the first large civilizations like that of the Egyptians. The artists that created Paleolithic paintings and sculptures

possibly belonged to groups marked by their intellectual and practical supe-riority. This line of thought, which seems promising, is sketched in Foley (1997, p. 73).

Major levels of an evolutionary (biological) grammar and the transition towards a culturally based grammar

From the stratified capacities and barriers discussed here, we can derive a first sketch of the grammar of a protolanguage. It specifies three hierarchical levels:

1   *stable* entities: no change in the perceptual and classificatory time window and recurrence as pattern (statistical relevance)
2   *dynamic aspects* of *entities* in change and motion ("force-dynamics")
3   the *bivalent* GRASP schema (capture or emission).

This allows for the accumulation of a lexicon of protonouns/-adjectives and protoverbs. The combinatorial possibilities depend on context. The grammar of the protolanguage is based on these protoclasses and their implicit dyna-mical binding forces (valences) and inherent causal links (force dynamics). The complexity barriers may explain why further conditions of control on the combinatorial/mapping/blending semantics had to be satisfied in order to arrive at a more complex and less context-dependent grammar. I have men-tioned three basic restrictions, which apply to protomanner adverbials, to a compact TMA component, and to recursive constructions of specifier phrases with a protonominal head.

COMPARATIVE BIOLINGUISTICS

If we want to understand human language, we cannot simply study animal behaviour, cognition, and communication. Since Jacob von Uexküll's pro-posals in his "*Bedeutungslehre*", far more radical comparisons have been made. These led to the field of "biosemiotics", which is characterized as follows:[5]

- The life sphere is permeated by sign processes and signification. Whatever an organism senses also means something to it.
- All organisms are born into a *semiosphere*, i.e., into a world of meaning and communication.
- The *semiosphere* places constraints or boundary conditions on the envi-ronment (Uexküll's "*Umwelt*").[6]
- It is plausible that the semiotic affordances and demands of populations were a decisive challenge to their success or even to their survival.

In this perspective, we can learn from very primitive animals and finally relate

the basic laws of sign behaviour to the origins of life (Wildgen, 2007a). This perspective may elicit enthusiasm or provoke rejection. In the case of mammals and primates, the parallels between human and animal behaviour are rather obvious, so that a systematic comparison seems promising. However, the Darwinian principle of continuity forces us to go beyond our immediate cousins and house pets to ask: What are the deeper principles in the realm of life that make communication and language possible or even necessary? It seems that beyond physical laws and chemical reactions, the facts of life refer to a new type of meaning, function, and purpose, which is characteristic of complex living systems. An important feature is that they operate simultaneously on different levels of magnitude. Thus one must be aware that the choice of a specific scale (from micro to macro) leads to very different insights concerning the living organism. What is extremely complicated (even chaotic) at a lower level (physical, chemical) may show a very regular (almost simple) organization at a higher level. René Thom (1974) suggested that the morphology of language is much simpler and in its organization more basic than the underlying neural or physiological morphologies. Even the physics of a process rendered by verbs like *run, catch, give, send, tie*, etc., are many orders of complexity beyond that of the linguistic patterns.

Contrary to reductionist views, the facts concerning the human mind and language are not beyond human grasp. They are the first things we can understand because we embody them. We are able to ask and answer questions concerning nature beyond our bodies only through symbolic competence. This creates an epistemological dilemma. Humans use their linguistic competence to do research in the natural sciences, but this competence cannot be assessed in the same way as questions in the natural sciences. This dilemma motivates a kind of garden path strategy in the humanities. First one starts in the direction of central concern: How can we understand human beings (ourselves)? This path ends after several steps and scientific progress becomes more and more difficult; the results are vague, insecure. Then using human symbolic competence, one returns to the analysis of physical, chemical, and biological aspects. With this apparatus one returns to the former garden path and hopes to move beyond the previous point of failure. One probably gets one step further, but must again undertake new expeditions into nature in order to take a third step down the garden path. Thus, learning from animals and from plants, biomolecules, chemical dynamics, etc. is a necessary strategy, but one should return to humans, their minds and language, even if the risk of failing along this path is daunting.

NOTES

1 The instrumental behaviour of chimpanzees living today shows elements of such a capacity. However, it remains, an open question whether the common ancestor of humans and chimpanzees had the same capacity (probably not).

2 This section is a partial, revised version of a paper presented at the Max Planck Institute for Evolutionary Anthropology in Leipzig on 29 May 2002; see http://www.fb10.uni-bremen.de/homepages/wildgen/pdf/evolutionarygrammar.pdf

3 In the evolution of pongids the origin of the precision grip seems to be a critical transition which allowed "grasping predation of certain species of insects at the terminal ends of bushes and shrubs" and this "opened a niche for primate evolution" (Quiatt & Reynolds, 1993, p. 123). It had as consequence the "conversion of active behaviour to crepuscular and diurnal phases of activity" (p. 123).

4 In the sense of Cassirer's "symbolic forms", technology already produces symbolic forms. Therefore, the impact on language would be a transfer between different types of symbolic forms (cf. Wildgen, 2004, p. 9).

5 Cf. Hoffmeyer (1996) and the definition of "biosemiotics" on his homepage: http://www.imbf.ku.dk/MolBioPages/abk/PersonalPages/Jesper/Hoffmeyer.html

6 Jakob Johann von Uexküll (1864–1944) worked at the Institute of Physiology, University of Heidelberg, and at the Zoological Station in Naples. In his book *Umwelt und Innenwelt der Tiere* (1909) he introduced the term "*Umwelt*" to denote the experienced world of an organism.

3   Vocal and gestural communication in nonhuman primates and the question of the origin of language

Adrien Meguerditchian and Jacques Vauclair

Human language is an extraordinary and unique means of communication, which involves complex cognitive functions like intentionality, generativity, elaboration, and comprehension of syntax, empathy, imitation, invention and manipulation of symbols, conceptual representations, categorization, referential cues, etc. In investigating the question of language origin, linguists often discount the views of primatologists, even though they have important contributions to make to the multidisciplinary effort necessary to deal with language evolution (Christiansen & Kirby, 2003; Hauser et al., 2002). Since nonhuman primates are phylogenetically very close to humans, research on our cousins can provide essential clues for inferring the features of our ancestral communication systems. Thus, a prime question for primatologists is to investigate whether direct precursors of language in the communicative behaviours of nonhuman primates.

Most studies in this domain pertain to the vocal modality and have produced controversial results. They have led some researchers to propose the existence of similarities between vocal communication and speech and to suggest that language resulted from the evolution of the vocal system in our ancestors (Ghazanfar & Hauser, 1999; Hauser, 1996; Snowdon, 2001a; Zuberbühler, 2005). However, over 30 years ago another ambitious theory— initially suggested by de Condillac (1746/1947)—received renewed interest. The anthropologist Hewes (1973) proposed that language first evolved from manual communicative gestures rather than from vocalizations. Some evidence for this gestural hypothesis is provided by the organization of speech. For example, we often gesture while we speak, signing the meaning of our words, e.g., bringing the index finger and the thumb close together while saying "small" (Goldin-Meadow & McNeill, 1999; McNeill, 1992). It is known that the gestural and vocal modalities are synchronized and that they share the same communicatory system (Bernardis & Gentilucci, 2006; Goldin-Meadow & McNeill, 1999). Moreover, the sign language of the deaf has essentially the same properties as speech and involves similar cerebral areas within the left hemisphere (Corina, Vaid, & Bellugi, 1992; Grossi, Semenza, Corazza, & Volterra, 1996; Kimura, 1993). This hemispheric lateralization is also evident for motor structures controlling both manual and oral movements

(Kimura, 1993; Iverson & Thelen, 1999). The evidence of links between speech and gestures has revived the hypothesis that language could have its roots in the gestural communication of our ancestors. A growing number of researchers advocate it (Corballis, 2002, 2003; Kendon, 1991; Kimura, 1993; Vauclair, 2004) and adduce studies performed with nonhuman primates in support.

We know that great apes use their hands and body to communicate with conspecifics in various social contexts. For example, a chimpanzee (*Pan troglodytes*) can effectively raise its arm as a request to be groomed by a social partner, slap the ground to threaten it, hold out its arm to make peace after a conflict, or—for juveniles—beg food from the mother by touching her mouth. Gestures of this sort have been described not only in chimpanzees (Goodall, 1986; Liebal, Call, & Tomasello, 2004; Tomasello & Camaioni, 1997; Tomasello, George, Kruger, Farrar, & Evans, 1985; Tomasello, Gust, & Frost, 1989), but also in gorillas, *Gorilla gorilla* (Pika, Liebal, & Tomasello, 2003; Tanner & Byrne, 1993, 1996), in bonobos, *Pan paniscus* (de Waal, 1988; Pika, Liebal, & Tomasello, 2005), in orangutans, *Pongo pygmaeus* (Liebal, Pika, & Tomasello, 2006), in siamangs, *Symphalangus Syndactulus* (Liebal, Pika, & Tomasello, 2004), and in three species of macaques (reviewed in Maestripieri, 2005). Generally, primatologists consider the functions of these gestures to be evolutionarily less essential than those expressed by vocalizations, which pertain to vital functions like defence/aggression, reproduction, discovering food, and avoiding potential dangers (Tomasello & Zuberbühler, 2002).

Since human language is not exclusively associated with the vocal modality, Fitch (2000b) proposed to distinguish the investigation of the origin of language in the broad sense, i.e., independent of communicative modality (vocal or gestural), from the investigation of the origin of speech, which requires identifying features related exclusively to articulated vocal language. In this chapter we review several major studies in nonhuman primates that possibly provide evidence for the main precursors of linguistic properties that are shared by both the gestural and the vocal modalities. These properties comprise flexibility of learning and use, intentional control and referential communication. Features associated exclusively with vocal articulated language will not be considered, e.g., the anatomy of the vocal apparatus, the acoustical traits of vocal signals, or the mechanisms of speech production and articulation. However, we will consider the neural substrate of gestural and vocal communication in nonhuman primates and examine the evidence for precursors of a left-hemispheric lateralization, which is typically involved in the control of speech. We will also discuss several studies on cognition, communication systems, and communicative behaviours in monkeys and apes in order to compare the main arguments for the gestural and the vocal theories of language origin.

THE FLEXIBILITY OF VOCAL AND GESTURAL SIGNALS

Human language is characterized by flexible acquisition and the use of shared conventions. The investigation of the flexibility of communicative signals in nonhuman primates may therefore help determine whether the vocal or the gestural modality is the more probable direct precursor of speech. We approach this question by discussing experimental studies carried out with great apes. One of the first studies was the unsuccessful attempt to teach speech to the chimpanzee Vicki (Hayes, 1952). After years of training, Vicki only managed to pronounce vocalizations vaguely resembling the words "papa", "mama", "up", and "cup". Other projects aimed at teaching apes gestures based on sign language were more successful. More than a hundred signs were learned by the chimpanzees Washoe (Gardner & Gardner, 1969) and Nim (Terrace, 1979), the gorilla Koko (Patterson, 1978), and the orangutan Chantek (Miles, 1990). Mastery of these signs shows the extra-ordinary capacity of apes to learn and flexibly use complex, manual signs to communicate with humans (Vauclair, 1996a). This stands in sharp contrast with apes' difficulties in mastering vocalizations.

Limited flexibility of vocal signals

Comparative psychologists and primatologists have found some evidence of flexibility in the vocal behaviours of nonhuman primates. Under different experimental conditions rhesus macaques (*Macaca mulatta*) could be trained to produce different types of their calls and to decrease the duration of their "coo" calls, even though they were not able to voluntarily modify the acoustic features of the calls (Sutton, Larson, Taylor, & Lindeman, 1973). Monkeys can increase the amplitude of their vocalizations when the environment is noisy (in common marmosets, *Callithrix jacchus*: Brumm, Voss, Köllmer, & Todt, 2004; in cotton-top tamarins, *Saguinus oedipus:* Roian-Egnor & Hauser, 2006). Furthermore, it has been demonstrated in various primate species that the acoustic structures of vocalizations change during development (reviewed in Roian-Egnor & Hauser, 2004).

Although such ontogenetic variations might be simply explained as the result of maturational processes rather than of vocal production learning (Fischer, 2002; Hauser, 1989; Seyfarth & Cheney, 1997), evidence of inter-individual differences in vocal behaviour related to variations in the social environment indicate that maturational processes are not the only possible factor in the flexibility of vocal expression. For example, the calls of male baboons (*Papio cynocephalus ursinus*) are shortened when their ranking position changes (Fischer, Kitchen, Cheney, & Seyfarth, 2004). In cotton-top tamarins social rank and reproductive state can influence the use of calls (Roush & Snowdon, 1994, 2000). Chimpanzees can produce different types of agonistic screams depending on their social role during a conflict (Slocombe & Zuberbühler, 2005a). In captive Campbell's monkeys

(*Cercopithecus campbelli*) variations in the acoustic fine structure of calls were observed in females throughout their adult life corresponding to significant social changes in their group (Lemasson, Gautier, & Hausberger, 2003). Using playback techniques, Lemasson, Hausberger, and Zuberbühler (2005) showed that the different variants were distinguished by other listening conspecifics. More impressively, Hopkins, Taglialatela, and Leavens (2007) demonstrated that 24 captive chimpanzees produced atypical vocalizations (an extended grunt involving the vocal tract or a splutter called "raspberries" performed with lips and mouth), especially in the presence of humans and out-of-reach food, which have never been described in wild groups. Moreover, the language-trained bonobo Kanzi used four additional vocalizations in a context of human communicative exchanges (Hopkins & Savage-Rumbaugh, 1991). Thus, great apes can use several novel vocal signals when raised in particular "ecological" circumstances, e.g., captivity, intense human interactions, out-of-reach food context, high-level social environment, etc.

Moreover, intergroup variations in some call features have been described between different matrilines of macaques (Gouzoules & Gouzoules, 1990; Hauser, 1992) and between geographically distant populations of wild chimpanzees (Arcadi, 1996; Mitani, Hasegawa, Gros-Louis, Marler, & Byrne, 1992), wild orangutans (van Schaik et al., 2003), macaques (Fischer, Hammerschmidt, & Todt, 1998; Sakura, 1989), and other monkey species (Hodun, Snowdon, & Soini, 1981; Rukstalis, Fite, & French, 2003). These data have led some authors to consider the existence of population-specific "dialects" in the vocalizations of nonhuman primates (Green, 1975; Mitani et al., 1992). Although it cannot be ruled out that population level variations might depend on genetic factors or on differences in the acoustic characteristics of the species' habitats (Mitani, Hunley, & Murdoch, 1999), several authors (Arcadi, 1996; Leavens, 2003) have suggested that a learning component within a group influences some traits of the acoustic structures of vocalizations. Several lines of evidence support this view. For example, the intergroup differences in the acoustic features of pant-hoot vocalizations in wild male chimpanzees reported by Crockford, Herbinger, Vigilant, and Boesch (2004) are found in neighbouring communities, but not in distant groups (separated by 70 km). This suggests that these variations could not result from genetic or habitat factors. Marshall, Wrangham, and Arcadi (1999) showed that within different groups of captive chimpanzees, individuals with similar vocal patterns were not kin-related. Moreover, the "trills" calls of pygmy marmosets (*Cebuella pygmaea*) tend to converge toward the same acoustic structure when individuals are put together in new groups (Snowdon & de la Torre, 2002; Snowdon & Elowson, 1999). Similar evidence has been reported in wild chimpanzees when two members chorused together (Mitani & Gros-Louis, 1998). In addition, the language-trained bonobo Kanzi has shown a capacity to modulate his vocal output according to the semantic context of his communicative interaction with humans (Taglialatela, Savage-Rumbaugh, & Baker, 2003).

Nonetheless, we suggest that flexibility in vocal production remains quite limited in nonhuman primates. With the exception of reports on novel vocal signals used in special circumstances with humans by captive chimpanzees (Hopkins, Taglialatela, & Leavens, 2007) and by a language-trained bonobo (Hopkins & Savage-Rumbaugh, 1991), there is, to our knowledge, no other evidence that monkeys and apes generate new vocal. Their vocal repertoire is fairly stable between groups within the same species. The reported variations of certain acoustic features are subtle and only concern existing, species-specific vocalizations. The fact that learning can play a role in the variations of vocal signals is not inconsistent with the hypothesis that vocal behaviours are primarily genetically determined. In other words, the vocal patterns of nonhuman primates' repertoires may be innate, but nevertheless subtly influenced by learning during the individual's lifetime owing to contextual and environmental social factors. Experimental studies support this hypothesis and illustrate these innate limitations. When rhesus and Japanese macaques' infants (*Macaca fuscata*) are cross-fostered, modifications of their species-specific vocal behaviour remain weak (Owren, Dieter, Seyfarth, & Cheney, 1992, 1993). The acoustic structures of vocalizations by hybrid gibbons, born from the crossbreeding between two different subspecies (*Hylobates lar* and *H. pileatus*), show patterns intermediate between those of the two parents (Brockelman & Schilling, 1984; Geissmann, 1984). The social or acoustical isolation after birth did not cause major changes in the vocal repertoire of rhesus macaques (Hammerschmidt, Newman, Champoux, & Suomi, 2000), black spider monkeys, *Ateles fusciceps robustus* (Eisenberg, 1976), or squirrel monkeys, *Saimiri sciureus* (Hammerschmidt, Freudenstein, & Jürgens, 2001, reviewed in Snowdon, Elowson, & Roush, 1997). The limited plasticity of the vocal communication systems of nonhuman primates thus casts doubt on reports of evidence of linguistic properties in their vocal system.

Ritualized gestures

Manual communicative gestures, which are particularly well-studied in the great apes compared to monkeys, are used more flexibly than vocalizations (Goodall, 1986; Tomasello & Zuberbühler, 2002). Indeed, individuals are able to invent new gestural signals to communicate with others (Goodall, 1986; Tomasello et al., 1985). The acquisition and use of some human-like gestures have often been reported in apes raised by humans (Tomasello & Camaioni, 1997). These gestures, which can be tactile, visual, or a source of sound, vary greatly not only among individuals in the same social group but also between populations, indicating the flexibility of this communication system (reviewed in Pika, Liebal, Call, & Tomasello, 2005). Depending on the individual, different gestural signals may be produced for the same goal and, conversely, similar gestures may be used in different contexts and to fulfil divergent goals (Tomasello et al., 1985; Tomasello et al., 1989). Tomasello (1996) explains this plasticity by suggesting that these gestures are individually learned via

"ontogenetic ritualization", rather than socially learned via imitation. In other words, each gesture seems to begin initially at an individual level from manual actions that become progressively ritualized in communicative signals during the subject's development. For example, when a chimpanzee, *A*, is groomed by a conspecific, *B*, *A* can come to raise its arm in order to facilitate the grooming of certain areas of its body by *B*. In the next step, *B* anticipates the "desire" of *A* to be groomed upon seeing its raised arm. Finally, *A* foresees the anticipation of *B* in performing the initial "arm-raising" behaviour in front of *B* in order to invite *B* to groom it. Although the flexibility of gestures' use in apes is much closer to speech properties than vocalizations, it must however be noted that these ritualization processes differ from the ritualization that is specific to speech acquisition in humans. In our species the learning of shared conventions is transmitted via social imitation during infants' development rather than through individual ontogenetic processes.

EMOTIONAL VERSUS INTENTIONAL CONTROL

Intentionality is a fundamental characteristic of language. Three criteria are usually cited in defining intentional communication in humans (Leavens, 2004a): (1) "attention-getting" behaviour, in which the signaller communicates only when an audience is present; (2) the visual orienting behaviour of the signaller is in phase with the social partner and a distal object or event of interest (alternation of gaze); and (3) when the social partner is not attending or responding, the signaller repeats his communicative cues (persistence of the signals). Several experimental and observational studies have been carried out in order to detect the presence of these criteria in nonhuman primates' communicative behaviours. In this domain gestures seem to provide more convincing evidence than vocalizations.

Are vocal productions intentional?

Most authors take the vocal productions of nonhuman primates to be under emotional control, e.g., fear for alarm call, excitement for discovering food, etc. After years of observing wild chimpanzees, Goodall (1986) concluded that "production of sounds in the absence of the appropriate emotional state seems to be an almost impossible task for a chimpanzee" (p. 125). In other words, primates may vocalize mainly automatically without specific intentions to inform a social partner. However, we cannot rule out that primates have some voluntary control over their vocalizations, even though such production may only be emotional. As reported above, their calls can vary according to particular changes in the social environment and Goodall observed that chimpanzees can inhibit expression of calls. Moreover, audience effects for vocal production, i.e., increase in rate of calls related to the

presence of conspecifics, have been reported for food calls in monkeys when discovering or sharing food (Caine, Addington, & Windfelder, 1995; Joyce & Snowdon, 2007), for "pant-hoot" in chimpanzees as a function of the proximity of their alliance partners (Mitani & Nishida, 1993), and for alarm calls in monkeys when predators appear (Cheney & Seyfarth, 1990a; Wich & Sterck, 2003). Most impressively, in response to a tiger (fake model) male Thomas langurs (*Presbytis thomasi*) continue to call until all conspecifics of the group have given an alarm call. They stop only after hearing the first alarm call of the last monkey. These results suggest the existence of a sophisticated audience effect (Wich & de Vries, 2006; see also Zuberbühler, 2006).

Although these vocal communicative behaviours satisfy the first criterion of intentional communication, "audience effect", further studies are needed to demonstrate the existence of intentional vocal signals in nonhuman primates. This question is particularly difficult to resolve in the case of vocal communication—in contrast to gestural communication, because we cannot tell whether vocalizations are being directed to a precise individual as easily as we can infer direction in gestures. Furthermore, to our knowledge, there is no convincing evidence that vocalizations could be dissociated from their emotional components. As we will see later, this interpretation is consistent with data concerning the cerebral substrate that controls the production of vocalization in monkeys.

Recent studies on captive chimpanzees have, however, revealed new results concerning whether vocal production could be under intentional control. Hopkins and colleagues showed not only an audience effect for vocal production in the presence both of an inattentive human and out-of-reach food (Hostetter, Cantero, & Hopkins, 2001; Leavens, Hostetter, Wesley, & Hopkins, 2004), but also a predominant use of two novel atypical vocalizations, while typical species-specific "food" calls were more frequent in the presence of food alone (Hopkins, Taglialatela, & Leavens, 2007). Such atypical vocalizations, produced especially in the presence of humans and food, were interpreted as signals used intentionally to capture the attention of the human (Hopkins, Taglialatela, & Leavens, 2007). This demonstration may be the first evidence of the generation of intentional vocal signals by captive great apes. However, this does not imply that the possible intentional properties of these atypical sounds can be generalized to the whole of chimpanzees' typical vocal repertoire or to other nonhuman primate species.

Dyadic gestures

In contrast to vocalizations, it is more easily acknowledged that gestural communications are under intentional control in apes (Bard, 1992; Call & Tomasello, 1994; Krause & Fouts, 1997; Leavens & Hopkins, 1998; Leavens, Hopkins, & Bard, 1996; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). Indeed, studies have demonstrated that their communicative gestures fulfil

the three criteria cited earlier. First, contrary to call production, all gestures are exclusively produced towards a specific recipient in order to elicit an appropriate behaviour from it (reviewed in Leavens, 2004a; Pika, Liebal, Call, & Tomasello, 2005). As in speech, gestures involve "dyadic" communications or even "triadic" in case of food begging, because this type of exchange between two partners also involves an external object, namely the begged food. Second, there are numerous descriptions of great apes' producing alternation of gaze between an experimenter and a requested object, especially when performing food begging or pointing gestures at the same time (Leavens & Hopkins, 1998, 1999). Third, the persistence of gestural signals when the recipients are not attending or not responding has often been observed in great apes. For example, captive chimpanzees produced repetitive food begging gestures when the experimenter did not deliver out-of-reach food (Leavens, Russell, & Hopkins, 2005). Moreover, "attractor" gestures are common in apes (Goodall, 1986). These gestures are used effectively to attract the attention of others when they are not attending or not responding (Tomasello, 2003), e.g., slapping the hand on the ground when a young gorilla wants to play (Pika et al., 2003) or shaking tree leaves when male chimpanzees want to show their sexual excitement to females (Goodall, 1986).

Additionally, the capacity of apes to adjust gestural behaviours to the recipient's attentional state has been clearly shown by the studies of Tomasello and colleagues. For example, in soliciting play young chimpanzees produced significantly more visual signals when the conspecifics were oriented to them and used auditory or tactile gestures when the recipients were inattentive (Tomasello et al., 1994; Tomasello et al., 1997). Other studies conducted in chimpanzees (Hostetter et al., 2001; Krause & Fouts, 1997; Leavens, Hostetter, et al., 2004; Liebal, Call, & Tomasello, 2004) and in all great apes species (Liebal, Pika, Call, & Tomasello, 2004; Liebal, Pika, & Tomasello, 2004, 2006; Pika, Liebal, & Tomasello, 2003, 2005) confirmed this finding. We know that great apes are also able to change their position to face recipients in order to communicate with them (e.g., Liebal, Pika, Call, & Tomasello, 2004). Thus, in transmitting their gestural signals, great apes are able to distinguish an attentive from an inattentive state of the audience based on the face and the body orientation of the recipient (in bonobos, chimpanzees, and orangutans: Kaminski, Call, & Tomasello, 2004; in chimpanzees: Hostetter et al., 2001; Leavens, Hostetter, et al., 2004). The role of eye contact in the communicative behaviours of nonhuman primates is more controversial (Call & Tomasello, 1994; Kaminski, Call, & Tomasello, 2004; Theall & Povinelli, 1999; review in Gómez, 1996). However, the most recent study on this question demonstrated with a large sample of 116 subjects that captive chimpanzees produced more gestural behaviours when the eyes of an experimenter with food were visible than when the experimenter's eyes were not visible (Hostetter, Russell, Freeman, & Hopkins, 2007).

REFERENTIAL COMMUNICATION AND THEORY OF MIND

The referential nature of communicative exchanges is an important property of language. We use the term "referential" for signals that refer to external objects or events. However, in using the concept of reference a distinction must be drawn according to whether the signal is gestural or vocal. We speak of "referential vocalizations" when they are semantically meaningful for the listeners, whereas "referential gestures" reflect the ability to voluntarily orient other individuals' attention towards an external object or event. These gestures do not imply symbolic representations, but their use suggests to some authors (e.g., Tomasello, 2006) some understanding of the mental states of others (Theory of Mind).

Meaningful vocalizations

Ever since the famous studies on alarm calls in vervet monkeys, *Cercopithecus aethiops* (Seyfarth, Cheney, and Marler, 1980; review in Cheney & Seyfarth, 1990b), it has been well established that monkeys produce distinct alarm calls according to the presence and the type of predator (eagles, leopards, and snakes) and that listeners respond with appropriate protective behaviour (Diana monkeys, *Cercopithecus diana*: Zuberbühler, 2000d; Zuberbühler, Noe, & Seyfarth, 1997; Campbell's monkeys: Zuberbühler, 2001; saddleback and moustached tamarins, *Saguinus fuscicollis*, *Saguinus mystax*: Kirchhof & Hammerschmidt, 2006; prosimians: Macedonia, 1990). This evidence has been corroborated by playback studies conducted in the wild, indicating that the recipients exclusively use the audited vocal signals to retrieve information about the category of predators. Furthermore, vocalizations in various monkey species, e.g., baboons, vervets, macaques, can also convey information about the identity of the caller and the nature of the social relationships among conspecifics (review in Cheney & Seyfarth, 1990b, 1990c). Playback studies demonstrated that monkeys not only exhibit abilities for vocal recognition of both individual and matrilineal kin (Cheney & Seyfarth, 1980, 1999; Hauser, 1991; Rendall, Rodman, & Emond, 1996), but also for extracting information from calls, e.g., indexical cues concerning body size and age (Ghazanfar et al., 2007), the respective dominance rank of the individuals engaged in a interaction (Bergman, Beehner, Cheney, & Seyfarth, 2003; Cheney, Seyfarth, & Silk, 1995) and in a conflict context the class of opponents and the level of physical aggression concerned (Gouzoules, Gouzoules, & Marler, 1984; Gouzoules & Gouzoules, 1989). In a study with great apes, after hearing conspecific vocalizations, a captive chimpanzee inferred the identity of the caller, selecting its corresponding photograph (Kojima, 2003). Finally, variation in vocal productions can be related to different categories of food. According to the quality of discovered food and the degree of excitement thus involved, toque macaques, *Macaca sinica* (Dittus, 1984), rhesus monkeys (Hauser, 1998; Hauser & Marler, 1993), and chimpanzees

(Hauser & Wrangham, 1987; Hauser, Teixidor, Field, & Flaherty, 1993; Slocombe & Zuberbühler, 2005b) vary the rates of their calls and such vocal patterns' variants can be meaningful for listeners, relating the appropriate categories of food to them.

However, these reports do not mean that the caller understands others' mental states or that these vocalizations are under intentional (as opposed to emotional) control. Although an audience effect was shown in such vocal behaviours, there is no evidence of theory of mind ability on the caller's part. In effect, in reacting to a predator, macaque females did not produce more alarm calls in the presence of ignorant offspring than in the presence of knowledgeable ones, indicating no attribution of knowledge to others (Cheney & Seyfarth, 1990a). Moreover, as noted by Premack (1972), Seyfarth and Cheney (2003), and Vauclair (1996a, 2003), it is incorrect to oppose affective and referential signals. An emotional vocalization can be strongly referential for listening individuals and, conversely, an intentional signal can provide information about the signaller's emotional state. The vocalizations of nonhuman primates can be compared with human babies' emotional, nonlinguistic cries, which are meaningful for parents insofar as they serve to alert them that, for example, the infant is hungry. We know that such emotional productions by humans can be independent of language abilities (Deacon, 1997). In other words, primates can simply vocalize in an emotional state reacting to external objects or events, while listeners extract information from vocal signals in learning to associate, by simple habituation, a type of vocalization with the appropriate social or environmental stimulus. Consequently, recipients appear to respond to the meaning of the signals rather than to their emotional intensity or to their acoustic features. Playback studies showed that rhesus macaques exhibit similar reactions to two acoustically different vocalizations, which refer to the same category of object (high-quality food; see Gifford, Hauser, & Cohen, 2003; Hauser, 1998; Hauser & Marler, 1993). This ability might indicate the existence of a conceptual representation of the information extracted from the emotional calls (see evidence for habituation effects in Cheney & Seyfarth, 1988; Zuberbühler, Cheney, & Seyfarth, 1999).

Such an associative learning ability on the basis of experience can explain why (1) juvenile vervet monkeys are less successful than adults in associating the corresponding predator with the distinct conspecific alarm calls (Hauser, 1988, 1989; Seyfarth & Cheney, 1986; review in Cheney & Seyfarth, 1990b) and (2) nonhuman primates are able to extract meaningful information from the vocalizations of other animal species. Diana monkeys understand the causes of chimpanzees' screams (Zuberbühler, 2000b) and infer the type of predator from the Campbell's monkeys' and guinea fowls', *Numida meleagris*, alarm calls (Zuberbühler, 2000c, 2000a). In addition, the bonobo Kanzi revealed an impressive ability for understanding English (Savage-Rumbaugh, 1990; Savage-Rumbaugh et al., 1993).

Pointing in nonhuman primates?

Observations and experiments conducted to evaluate nonhuman primates' abilities to produce referential gestural signals have produced controversial results (review in Gómez, 2005; Leavens, 2004a; Pika, Liebal, Call, & Tomasello, 2005; Tomasello, 2006). Are great apes able to use their gestures to draw the attention of other individuals to an external object, an event, a direction, or a location? In other words, are they able to point? Some recent investigations support such an interpretation. Pika and Mitani (2006) have described a surprising gesture in wild chimpanzees during mutual grooming behaviours in which the signaller scratches a part of its body in order to show to its social partner the precise area that it wants to have groomed (see Figure 3.1).

In addition, in front of a human, captive chimpanzees are able to direct their arm towards one of two out-of-reach opaque bottles where food is hidden (Leavens, Hopkins, & Thomas, 2004). Moreover, pointing gestures performed with humans have been frequently reported not only in captive chimpanzees, but also in other captive great apes and in some monkey species (Leavens & Hopkins, 1999; Gómez, 2005). During the production of these communicative gestures, evidence of attention-getting and gaze alternating behaviours are common, especially in great apes (Leavens & Hopkins, 1999).

However, pointing has never been described in wild populations or between conspecifics. It might result from "ontogenetic ritualization" in relation to their interactions with humans and restrictive captivity conditions because they need to interact with humans in order to access out-of-reach food (Leavens, Hopkins, & Bard, 2005). According to some researchers, characterizing such gestures as pointing or as referential in nature is unadvised
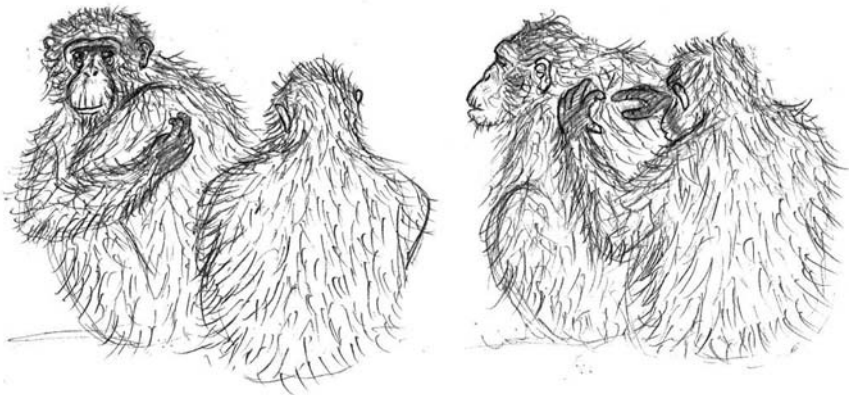
Figure 3.1 Referential manual behaviours in wild chimpanzees. A chimpanzee is groomed by a social partner, after having scratched a part of its body in order to show to the recipient the precise area that it wanted to be groomed. Such behaviours indicate a shared understanding of the gestural orienting signal that is typical of referential communication (Pika & Mitani, 2006). Drawing © Adrien Meguerditchian.

(Gómez, 2005) or even incorrect (Baron-Cohen, 1999; Povinelli, Bering, & Giambrone, 2003; Tomasello, 2006). In view of the fact that using referential gestures implies some understanding of others' mental states, these researchers stress that apes do not seem to comprehend pointing (but see Miklósi & Soproni, 2006) or the other's underlying intention. Thus, in this view these gestural productions might be better explained by apes' capacity to associate a gestural signal with the desired goal via an "ontogenetic ritualization" process, rather than through the ability to attribute mental states to others.

In addition, only specific goals—"obtaining food" or "obtaining this object"—motivate the use of such gestures. Indeed, all communicative gestures in nonhuman primates are exclusively "imperative"[1] insofar as they always express requests or demands. And in contrast to language, in which linguistic signals can be also declarative[2] or used to inform another person about the location of an object (Liszkowski, 2005), nonhuman primates are apparently not able to communicate simple discoveries or information to others with gestures as we do when we say: "Look at this stone!" or "The object that you're looking for is here". Thus, the capacity of apes to manipulate the attention of a recipient towards external events through gestures seems limited.

However, the observations of Pika and Mitani (2006) in wild chimpanzees showed that the recipient of gestural signals understood the meaning of the directed scratch gestures performed by his social partner, who wanted to be groomed in a specific area. In most cases the recipient reacted by orienting its grooming behaviour towards the area indicated by the signaller and this orientation might be evidence of typical referential behaviour. Moreover, it has been demonstrated that great apes understand the importance of the visual modality in the experimenter for transmitting their gestural signals (Call & Tomasello, 1994; Gómez, 1996; Hostetter et al., 2007). They appear to have a certain understanding of what others do and do not see (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001, 2006; Tomasello, Call, & Hare, 2003). On our point of view such high-level cognitive processes could well be involved in producing these gestures and may thus be considered a reliable prerequisite for referential communication. In conclusion, we suggest that the properties of these gestural signals constitute an essential, first evolutionary step for the emergence of speech and theory of mind.

THE VOCAL COMMUNICATION SYSTEM AND THE BRAIN

Since the work of Broca (1865) and Wernicke (1874), we know that most language functions are under the control of the left cerebral hemisphere and involve a complex neural network in which Broca's and Wernicke's areas play a key role. Thus, the question of the lateralization and the localization of the neural substrate involved in gestural and vocal communication in nonhuman primates is crucial for evaluating the potential continuities in the hemispheric

specialization for human language and thus for determining the best candidate for direct precursors of speech.

Behavioural asymmetries studies linked to the production and perception of vocalizations

Several studies have investigated hemispheric lateralization for vocal control in nonhuman primates via indirect studies of behavioural asymmetries. In humans, the right side of the mouth opens first and wider, indicating left hemispheric dominance for language control (Graves, Goodglass, & Landis, 1982; Wolf & Goodale, 1987). Thus, Hook-Costigan and Rogers (1998) evaluated the asymmetries of mouth expressions during call production in marmoset monkeys and reported (at a population level) a larger right side of the mouth/left hemisphere bias in producing social contact calls (positive emotional signals) and a larger left side of the mouth/right hemisphere bias in producing fear expressions (negative emotional signals) with or without vocalizations. The authors hypothesized that the asymmetry of call production could be due to the emotional valence of the signal. However, the results of a similar study in rhesus monkeys by Hauser and Akre (2001) do not support this hypothesis. These authors reported that the left side of the mouth opened first (right hemisphere bias) in producing all types of calls (including both negative and positive emotional signals). Thus, these findings may not express a human-like behaviour that relates to linguistic abilities, but rather emotional processing in which the right cerebral hemisphere is more involved.

The reported results of indirect behavioural asymmetries studies conducted on the *perception* of vocal signals by monkeys do not conform to the patterns obtained for the *production* of calls. Using the dichotic listening paradigm, Petersen, Beecher, Zoloth, Moody, and Stebbins (1978) found that all five Japanese macaques tested, unlike the other monkey species exposed to the same Japanese macaque's calls (except one vervet monkey), discriminated two species-specific vocalizations faster and more accurately with the right ear than with the left ear. This finding led the authors to suggest a left hemispheric advantage for processing conspecific calls, but not for processing heterospecific vocal signals. Such perceptual asymmetries may be then attributed to the functional significance of the conspecific calls rather than to the acoustic features of the signal.

Hauser and Andersson (1994) reached the same conclusion, using a different behavioural paradigm in 80 rhesus monkeys. They measured the asymmetries of head orientation to different vocal signals emitted from a speaker behind the subject. The authors reported a population level right ear advantage for species-specific vocalizations, but not for a heterospecific call (a local bird call). These data suggest that a left hemispheric advantage could be at work for processing conspecific calls (Hauser & Andersson, 1994) on the basis of the calls' temporal features like interpulse intervals and the amplitude

envelope shape (Ghazanfar, Smith-Rohrberg, & Hauser, 2001; Hauser, Agnetta, & Perez, 1998). However, recent studies using the same procedure on two other phylogenetically close primate species produced contradictory results. Gil-da-Costa and Hauser (2006) showed that five vervet monkeys presented a population level left ear/right hemisphere advantage for processing species-specific vocalizations but no behavioural orienting asymmetries for other auditory stimuli (nonbiological sounds and heterospecific calls), whereas no bias was observed in a sample of 55 Barbary macaques, *Macaca sylvanus* (Teufel, Hammerschmidt, & Fischer, 2007). Such contradictory findings between phylogenetically close primate species (vervet monkeys, rhesus, Japanese and Barbary macaques are all members of the *Cercopithecidae* family) call into question either (1) the reliability of this behavioural paradigm (or some of its methodological aspects) for evaluating the hemispheric lateralization involved in the perception of vocal signals, or (2) the argument for a continuity between nonhuman and human primates concerning the neural bases for processing conspecific vocal signals. Further investigations are needed to clarify this point.

Neurobiological investigations of vocal perception

Neurobiological studies can shed some light on the point raised above (Ghazanfar & Hauser, 1999; Taglialatela, 2007). First, in some monkey species populations of cortical neurons (in the superior temporal gyrus, STG[3]) are selectively activated in processing species-specific vocalizations. Indeed, recording single-unit activity in squirrel monkeys showed that 80–90% of the neurons in the STG responded differentially to conspecific calls (Wollberg & Newman, 1972). Other studies on the auditory cortex of rhesus macaques (Rauschecker, Tian, & Hauser, 1995; Tramo, Bellew, & Hauser, 1996) and marmoset monkeys (Wang, Merzenich, Beitel, & Schreiner, 1995) support these findings. These studies raise two questions concerning the issue of language origin: (1) Is the neural circuit involved in processing monkeys' calls related to a left hemispheric lateralization like speech? (2) Does it involve some homologous language areas?

Earlier research on macaques using lesions in the left temporal lobe and left auditory cortex showed alteration of the subjects' performance for vocal processing tasks, thus supporting a functional dominance of the left hemisphere for vocal perception (Dewson, 1977; Gaffan & Harrison, 1991; Heffner & Heffner, 1984). More recently, the use of brain imaging techniques (positron emission tomography, PET) with rhesus monkeys corroborated these findings. Thus, Poremba et al. (2004) demonstrated greater metabolic activity within the STG in the left dorsal temporal pole (compared to the right) with species-specific vocal stimuli, but a right hemispheric dominance in other parts of the STG for other sounds. The authors raised the question of whether this high-level auditory processing area, functionally lateralized in the left hemisphere, could be a precursor of the language area in humans.

Concerning this key point, a new study with rhesus monkeys using a tomographic brain imaging technique has reported the implication of the posterior part of the STG and the F5 area (ventral premotor cortex, PMv) with a dominance of the right hemisphere for processing monkey's calls (Gil-da-Costa et al., 2006). These cerebral regions, which the authors consider homologous to Wernicke's and Broca's areas in humans, belong to areas that responded better to two species-specific vocalizations than to other auditory signals. These results led Gil-da-Costa et al. (2006) to propose a continuity between the neural processing of conspecific calls in monkeys and the neural circuits involved in human speech. However, Ghazanfar and Miller (2006) have criticized this view by pointing out methological shortcomings of the approach and noting that the report of right hemispheric dominance for call processing diverges from the left lateralization that is characteristic of language.

Neurobiological investigations of vocal production

The investigation of the neural circuit for production of vocalizations in nonhuman primates is essential for evaluating potential continuities with the cortical cerebral substrate of human speech. The available studies concern only monkey species and have shown that production of vocal signals is exclusively related to the limbic system or to structures connected to it (notably in regions related to the control of emotions in the human brain, but not to homologous language areas: Jürgens, 2002; Ploog, 1981). In rhesus monkeys Aitken (1981) reported that ablation of the homologue of Wernicke's and Broca's areas did not affect vocal behaviours, whereas lesions of the anterior cingulate cortex did. In squirrel monkeys only electrical stimulations performed in limbic and subcortical structures were able to induce vocalizations, whereas the stimulation of homologous language areas or other cortical regions did not (see Ploog, 1981). Additionally, the hemispheric lateralization for the control of vocal production via the investigation of the neural substrate remains unclear in nonhuman primates. Indeed, Jürgens and Zwirner (2000) demonstrated a lateralization of the vocal control in squirrel monkeys at the individual level, but not at a population level. To our knowledge, there is no evidence of such asymmetries in the literature and we have seen here that the combined findings of behavioural studies (asymmetries of mouth in call production) have led to contradictory patterns of laterality. In brief, the available findings do not support the hypothesis of a continuity between the lateralization of calls in nonhuman primates and the left-lateralized neural system of human language.

THE GESTURAL COMMUNICATION SYSTEM AND BRAIN

Asymmetries of communicative gestures

In humans the preferential use of one hand in most manual activities is linked to the dominance of the opposite cerebral hemisphere. Approximately 90% of humans are right-handed and this bias reflects a left hemispheric lateralization for hand control (Annett, 1985). Right-handedness is clearly linked to the left-hemispheric specialization for language functions (Knecht et al., 2000). Moreover, the activity of the right hand is predominant (1) for manual movements when people are talking (Kimura, 1973), (2) for signing in the deaf (Vaid, Bellugi, & Poizner, 1989), and (3) for pointing gestures by infants during speech development (Blake, O'Rourke, & Borzellino, 1994); this, reflects a left-hemispheric lateralization for the production of gestures related to language. Some studies in nonhuman primates have investigated manual asymmetries of gestural communication in order to infer functional hemispheric specialization for the production of gestures. Is this communication system lateralized in the left-hemisphere like human language? Are nonhuman primates mostly right-handed for gestures?

The first studies in this domain concerned signing or pointing in language-trained great apes (the gorilla Koko: Shafer, 1988; the orangutan Chantek: Miles, 1990; several chimpanzees: Krause & Fouts, 1997; Morris, Hopkins, & Bolser-Gilmore, 1993; Steiner, 1990), and nonlanguage trained chimpanzees (Leavens et al., 1996). However, the samples were too small to reliably investigate representative population-level hand use/hemispheric bias and presented several contradictory results (review in Hopkins & Fernandez-Carriba, 2002). Studies of spontaneous, species-specific gestures in captive apes revealed a bias for a right-hand use in 20 bonobos (Hopkins & de Waal, 1995), but no population-level manual bias in 16 chimpanzees for clapping gestures (Fletcher, 2006). But here, also, the size of the samples in these reports is insufficient to infer reliable hand preferences at a group level.

The first studies on chimpanzees' communicative gestures with large samples (above 100 subjects) showed significant population-level right-handedness for holding out the hand in presence of an human experimenter to request or point to out-of-reach food (Hopkins & Cantero, 2003; Hopkins & Leavens, 1998; Hopkins et al., 2005; Hopkins & Wesley, 2002). Compared to asymmetries of gestures produced alone, the degree of preference for the right hand was greater when the gestures were performed simultaneously with atypical novel vocalizations (Hopkins & Cantero, 2003). This indicates that the left hemisphere may be more activated when producing gestures and these novel vocalizations simultaneously. This finding could be the first demonstration that some vocal signals involve a left hemispheric lateralization when they are inserted into a gestural system. We suggest that this left hemispheric dominance, which has never before been reported for vocal production, could be related to the possibly singular intentional features of such atypical

vocalizations in captive chimpanzees (Hopkins, Taglialatela, & Leavens, 2007). Interestingly, in human infants the right hand is more strongly involved than the left when associated with the production of repetitive vocal-motor activity during the babbling phase (Locke, Bekken, McMinn-Larson, & Wein, 1995). The degree of right-handedness for pointing gestures has also been shown to increase during speech development (Blake et al., 1994). Thus, Hopkins and Cantero's (2003) results suggest the interesting hypothesis that there is a preadaptation for a communicatory intentional bimodal system (vocal and gestural), lateralized in the left hemisphere of chimpanzees, which is similar to the pattern described for language (Kimura, 1993).

The first investigation of communicative gestural asymmetries in monkey species was conducted with 60 captive baboons (*Papio anubis*), living in social groups (Meguerditchian & Vauclair, 2006). The species-specific gestural behaviour studied consists in a repetitive slapping or rubbing of the hand on the ground towards a focused subject (a conspecific or the human observer) in order to threaten or intimidate it (see Kummer, 1968, for the first description of this gesture; Figure 3.2).

The results showed a strong and significant preference for the right-hand at the population level for both intra- and interspecific threat gestures. Interestingly, these patterns of laterality differed from those reported in noncommunicative manipulative motor actions in baboons (Vauclair, Meguerditchian, & Hopkins, 2005). We showed that (1) hand preferences for gestures did not correlate with hand use for motor tasks within the same individuals, and (2) the degree of population-level right-hand bias reported for communicative gestures was stronger than that obtained for a coordinated bimanual task (Meguerditchian & Vauclair, 2006). Moreover, a similar absence of correlation has been described in chimpanzees (Hopkins & Wesley, 2002). A similar difference in the degree of right-handedness between communicative and manipulative tasks was exhibited both in chimpanzees (Hopkins et al., 2005)
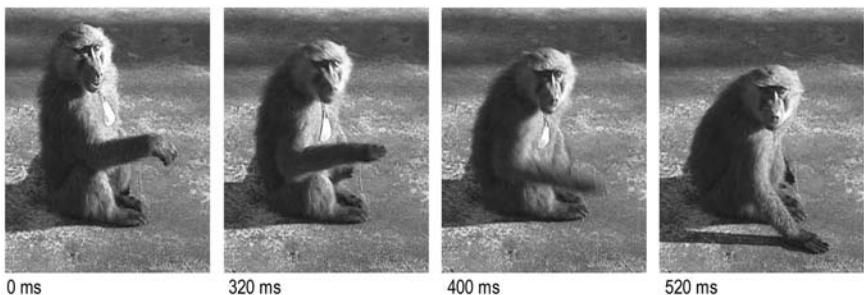
Figure 3.2 An intentional communicative gesture performed by a baboon. A young male intimidates a human observer by quickly slapping his right hand on the ground. A predominance of right-handedness at a group level has been measured, suggesting thus a left-hemispheric lateralization for gestures' production (Meguerditchian & Vauclair, 2006). Time is indicated in milliseconds (ms). Photograph © Adrien Meguerditchian.

and in children raised by deaf parents (Bonvillian, Richards, & Dooley, 1997). Such findings suggest the existence of a communication system (different from the one involved for manipulative actions), which is lateralized in the left hemisphere and involved in producing gestures.

These combined reports suggest a continuity between baboons, chimpanzees, and humans for left-hemispheric specialization. We have argued elsewhere that lateralization for language may have evolved from a gestural system of communication, lateralized in the left hemisphere in their common ancestor at least 30 million years ago (Meguerditchian & Vauclair, 2006).

The neural substrate of gesture production and the mirror-neurons system

To verify the continuity hypothesis proposed previously, it is essential to determine whether the lateralized gestural communication system implicates homologous language areas in the brain of nonhuman primates. The available research on this question is encouraging.

First, Cantalupo and Hopkins (2001) using structural MRI techniques scanned the brains of 20 chimpanzees and showed that Broadman's area 44 (equivalent to Broca's area) was larger in the left hemisphere than in the right. Moreover, Hopkins and Cantalupo (2003) found a correlation between the predominant use of the right hand for communicative gestures and the left-hemispheric asymmetry of area 44. Furthermore, Petrides, Cadoret, and Mackey (2005) reported that in monkeys, stimulation of a homologous region of Broca's area (area 44) induced hand and lip movements. This finding underscores the connection between manual and facial gestures. More recently, in 56 chimpanzees Taglialatela, Cantalupo, and Hopkins (2006) found a significant correlation between right-handedness for manual communication and the left asymmetries reported in the inferior frontal gyrus[4] (homologous to the language area involved in humans during pronunciation of deictic sentences; Loevenbruck, Baciu, Segebarth, & Abry, 2005). These findings may reveal a continuity between the neural bases of gestural communication in chimpanzees and the neural circuits of language production in humans. They strengthen the hypothesis that language may have evolved from a gestural system of communication lateralized in the left hemisphere in the common ancestor of chimpanzees and humans at least five to seven million years ago (Hopkins et al., 2005; Taglialatela et al., 2006). Further studies with baboons and other primate species, using behavioural and MRI techniques, are necessary in order to support the hypothesis of a similar continuity with this Old World monkey species (Meguerditchian & Vauclair, 2006).

Second, a major discovery in recent cognitive neurosciences, using recording of single-unit neuron activity, has revealed the existence of "mirror neurons" in the F5 area (homologous to Broca's area) in the prefrontal cortex of macaque monkeys. These neurons are activated not only when the monkey is performing a manual action, e.g., cracking nuts, but also when the subject

observes (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) or hears (Kohler et al., 2002) the same action carried out by another monkey or by a human. In addition, when the subject observes communicative oral gestures like lip-smacking or lip protrusion performed by an experimenter, other populations of neurons in the F5 area discharge (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). This latter finding demonstrates the neuronal links between the oro-facial and the manual systems involved in communication. Thus, nonhuman primates could have the capacity to recognize and build mental representations of the intentions and of the manual/facial actions of others. The ability to share an understanding of gestural intentions may have been an ideal substrate for the emergence of language and for the attribution of mental states to others (Arbib, 2005; Rizzolatti & Arbib, 1998). We note, however, that other authors reject the idea that the mirror neuron system is a suitable basis for the emergence of language (Jacob & Jeannerod, 2005).

DISCUSSION

Within the broad question of the origin of language, investigations of non-human primates' communication systems have uncovered possible continuities with some properties of human language, which nonetheless are highly contested. This review of some major studies has addressed the features of gestural and vocal modalities in our primate cousins respectively. At this stage of research we think that the prospects for establishing a relevant substrate for the emergence of language are less promising for vocal systems than gestural ones.

First, although it has been frequently reported that the vocal control in monkeys and apes affords some plasticity (see pp. 63–64), this flexibility remains limited compared to the flexibility of human language. The vocal features seem to be mostly genetically determined, despite the subtle and small influence of learning over an individual's lifespan. On the other hand, a limited ability to create new vocal signals in their repertoire, may not be regarded as an especially serious limitation in investigating the precursors to human language in the vocal system of nonhuman primates. In effect, in developing language, "what humans have is the ability, not particularly to create novel sounds per se, but to use a set of sounds in different combinations to create novel sequences of sounds that form words and ultimately phrases and sentences" (Snowdon, personal communication, 7 April 2007). From this perspective the study of combinations of calls, their flexibility and their meaning in monkeys and apes might be the most appropriate approach for investigating language origins. However, the few findings available on this topic are not particularly convincing (see later).

Second, there is no evidence that vocal production in nonhuman primates is intentional or that vocalizations can be dissociated from emotional control (see pp. 66–67), despite remarkable capacities to extract some semantic

information from vocal signals. However, an exception must be noted in captive chimpanzees with the reports of the use of two novel sounds especially in the presence of both humans and out-of-reach food. These atypical productions in a great ape may be the unique vocal signalling used voluntarily to get the attention of humans.

Third, it is well established that these vocalizations are meaningful and referential for listening monkeys and apes, as words are for listening humans. Vocal signals can indeed refer to the type of food, to the nature of predators or to the identity, the kin, and the social rank of the caller (see pp. 69–70). However, it is likely that this evidence does not reveal a similarity between the nature of primates' calls and the nature of words, but rather reveals the capacities of nonhuman primates to learn to associate, by simple conditioning, a perceived vocal signal, e.g., an emotional call, with the appropriate physical or social environmental stimuli, i.e., predators or food. Moreover, primates can also extract information from heterospecific vocalizations. It is worth noting that such a capacity has also been demonstrated in hornbills which reacted only to the Diana monkeys' alarm calls related to their specific predator (Rainey, Zuberbühler, & Slater, 2004a, 2004b) and in domestic dogs (*Canis familiaris*), which associated the corresponding object with the word produced by the experimenter (Kaminski, Call, & Fischer, 2004). Since primates, dogs and hornbills, do not have naturally meaningful calls, such conditioning processes in animals for extracting information from vocal signals are independent of their species-typical communicative vocal production system. The representational and categorization abilities that may be involved in nonhuman primates' understanding of vocalizations (Russ, Lee, & Cohen, 2007; Zuberbühler et al., 1999) could represent the precursor to the representational processes involved in human language (Vauclair, 1996a, 2003). In other words, it is not monkeys' and apes' vocal communication that might present a continuity with language here, but rather high-level cognitive processes involved in understanding and categorizing the physical and the social environments. More specifically, the fact that baboons can master and represent social rules, hierarchical relationships, identity of callers, or their dominance rank by observing an interaction (Kummer, 1978) or by hearing vocalizations (Bergman et al., 2003; Cheney et al., 1995; Cheney & Seyfarth, 1999), led Seyfarth, Cheney, and Bergman (2005) to propose that "the mechanisms underlying language might have evolved from the social knowledge of our pre-linguistic ancestor" (p. 264), rather than from vocal behaviours.

This interpretation, which supports the existence of an amodal representational process for understanding vocal signals, is congruent with the results of a neurobiological study in rhesus macaques. In effect, Gil-da-Costa et al. (2004) reported that playback of salient conspecific vocalizations evoked neural activity in multimodal-related regions: visual, auditory, and affective processing areas (regions from the limbic system related to memory encoding). Pointing out that this neural circuit corresponds to the human neural network associated with conceptual representation, the authors argue for the

involvement of an amodal conceptual system in monkeys for processing meaningful vocalizations; they claim that such a substrate may be the precursor of the representational processes implicated in human language. These abilities in nonhuman primates also seem to be independent of their vocal production system and cannot be specifically regarded as a direct precursor of speech production in humans.

In fact, there is a general lack of evidence for continuity between human and nonhuman primates concerning the neural substrate of the vocal modality. In accord with the distinction drawn between comprehension of calls, which appears language-like, and their production, which is not like language, the available neurobiological and neuroethological studies reveal a similar, important distinction between the neural circuits involved in the *perception* of vocalizations and the neural substrate of vocal *production* in monkeys. As in humans for language processing and in other species like mice (Ehert, 1987), rats (Fitch, Brown, O'Connor, & Tallal, 1993), and California sea lions (Böye, Guntürkün, & Vauclair, 2005), a left hemispheric dominance for the perception of species-specific calls has been frequently reported in monkeys. Moreover, some studies revealed the involvement of high-level cortical structures of the brain, especially within the STG (and maybe homologous language areas: Gil-da-Costa et al., 2006). A left-hemispheric dominance has never been reported for vocal production in contrast to perception (but see the possible exception of atypical attention-getting vocalizations in captive chimpanzees; Hopkins & Cantero, 2003). Indeed, in contrast to human language, vocal control in nonhuman primates seems to imply nonlateralized subcortical structures (limbic or cingulate system). This strengthens the argument for the emotional control of call productions (Jürgens, 2002; Ploog, 1981).

Notably, recent evidence has contradicted the hypothesis of a left-hemispheric dominance for call perception in primates: The combined findings on behavioural orienting asymmetries of vocal processing in monkeys are contradictory (see pp. 73–74) and the functional right hemispheric dominance reported by Gil-da-Costa et al. (2006) contrasts with the previous neurobiological investigations of vocal perception (Dewson, 1977; Heffner & Heffner, 1984; Poremba et al., 2004). In addition, serious criticisms have been made concerning the methodology (Hopkins and Fernandez-Carriba, 2002; Taglialatela, 2007) and the robustness of the results in the studies which reported left hemispheric dominance for call processing. Further studies in different nonhuman primate species are necessary to clarify these points and to determine whether the results between and within the two indirect (behavioural) and direct (neurobiological) approaches can be made congruent. The observed disparities in the available studies may be reconcilable, if we consider that for a given vocal stimulus the pattern and direction of the asymmetrical responses can vary according to the type of information (conceptual, emotional component) extracted by the subject. Indeed, we have emphasized that a subject's ability to extract meaningful information from a vocal signal can vary as a function of its understanding of the social and

physical environment and the social context in which the vocalization is produced. Consequently, these further investigations should take into account the possible interindividual variations concerning the communicative salience of sounds presented to subjects in such paradigms (Taglialatela, 2007).

Finally, we note that there are few behavioural and neurobiological investigations concerning the great apes' vocal system, compared to the knowledge available on monkeys. This situation is unfortunate, because apes are phylogenetically closer to humans than monkeys and are consequently the more interesting model for discovering precursors of language. This lack of data limits the speculations about the potential continuities between nonhuman primates' communicatory systems and human speech.

Studies on the gestural modality of nonhuman primates seem to present a fruitful line of investigation for identifying the precursors of language. The findings reviewed suggest that gestural communication and human language share certain properties. Gestures might be referential in some circumstances and, contrary to vocalizations, the production of such gestural signals is dyadic, clearly intentional and highly flexible. Moreover, Pollick and de Waal (2007) demonstrated in bonobos and in chimpanzees that in contrast to vocal and facial signals gestural behaviours exhibited significant independence from specific behavioural contexts, indicating greater flexibility of the gestural communication system in apes.

Moreover, the production of gestures may involve a left hemispheric lateralization according to the predominance of the right hand for gestural communication reported in chimpanzees (Hopkins et al., 2005) and in baboons (Meguerditchian & Vauclair, 2006). Interestingly, such right-hand preferences are correlated with left-neuroanatomical asymmetries reported for homologous language areas in chimpanzees (Taglialatela et al., 2006). These data support the view that language may have evolved from an ancestral intentional communicative gestural system lateralized to the left hemisphere. The vocal system might have been progressively inserted into the gestural system, become intentional and in this way left-lateralized during language evolution (Corballis, 2002). This incorporation is suggested by evidence of the increasing predominance of the right hand/left hemisphere in chimpanzees, where novel vocalizations are emitted simultaneously with manual begging for food from a human (Hopkins & Cantero, 2003). Thus, the communication system could have become bimodal to finally come under the dominance of the vocal modality (speech) in humans, as it is currently. In this view manual gestures during speech production might constitute the residual part of this bimodal communicatory system (McNeill, 1992).

Additionally, the discovery of mirror neurons in a homologue of Broca's area underscores the major role of gestures in action understanding and in interindividual communication. These neurons discharge both for the production and the perception of intentional actions (manual/facial). Since mirror neurons are present in humans (see Gentilucci & Corballis, 2006) and involved in speech functions, evidence of this neural ability in monkeys supports the

view that the mirror system could have been used in our prelinguistic ancestors for intentional gestural communication during language evolution (Arbib, 2006; Rizzolatti & Arbib, 1998). To our knowledge, there is no study yet showing that mirror neurons are involved in vocalizations and this might be an interesting area for future research.

Other sets of data highlight the central importance of manual actions as preadaptations for the emergence of language. Koechlin and Jubault (2006) demonstrated that Broca's area is involved in all temporally sequenced, hierarchical human actions. This finding suggests that language could have its roots not only in manual communication, but also in the complex sequential manipulative actions performed by our ancestors, e.g., tool use. This hypothesis was advanced (Bradshaw & Rogers, 1993; Greenfield, 1991) with the idea that lateralization of hand use could have been selected in our ancestors for such a task and could constitute a precursor for language lateralization. Results of a recent study with apes support this hypothesis. Hopkins, Russell, and Cantalupo (2007) showed that handedness in chimpanzees for tool use, unlike other motor actions, correlates with neuroanatomical asymmetries in homologous regions of language areas (the planum temporal and the frontal-orbital sulcus).

Moreover, Ferrari, Rozzi, and Fogazzi (2005) demonstrated that mirror neurons located in a section of premotor area F5 in pig-tail monkeys (*Macaca nemestrina*) responded to the observation of the use of tools by an experimenter. These hierarchical and sequential behaviours are necessary for language (notably in grammar for processing hierarchical relations of information in a temporal sequence: Koechlin & Jubault, 2006). However, the respective roles of manual communication and complex motor behaviours like tool use in the preadaptation for the emergence and lateralization of language are still unclear. Nevertheless, they suggest new avenues for exploring the evolution of language.

Many questions remain unanswered. For example, several studies have reported close relationships between hand and lip movements and homologous regions of Broca's area (Ferrari et al., 2003; Petrides et al., 2005). One study also revealed that chimpanzees' fine motor actions are accompanied by sympathetic mouth movements (Waters & Fouts, 2002). These studies investigate the role of the facial system during the evolution of language compared to the manual and vocal systems. Given that speech implies complex sequential oral gestures, we suggest that the facial system might constitute a relevant mediator between the gestural communication system and speech. On the assumption that the basic structure of syllables derives from the succession of constrictions and mouth openings involved in chewing, sucking, swallowing, and visuofacial communicative cyclicities like lipsmacks, MacNeilage (1998) proposed the "frame-content" theory of speech. For MacNeilage the basic components of speech—an oscillatory (frame) and a segmental (content)—have their source in cyclic activities of ingestion in our ancestors. In considering this hypothesis, we can suggest with Arbib (2005)

that ingestive behaviours were progressively ritualized in orofacial (lipsmacking) and gestural communication in monkeys. Gentilucci and Corballis (2006) have speculated that facial elements were gradually introduced with vocal elements into the gestural system during language evolution. Further studies in nonhuman primates are clearly needed to understand the role of facial communication and its relationship to the system that finally led to speech.

Another field to be explored concerns the phylogeny of syntax, one of the major properties of human language. Whether precursors of grammatical rules can be found in primates' communication systems remains unclear. The available studies are few in number and mainly concern the vocal modality. For example, using a habituation/dishabituation paradigm, Fitch and Hauser (2004) showed that cotton-top tamarins reacted to the modification of simple syntactic rules from playback artificial auditory patterns. However, their competence is limited to simple iterative rules ("finite state grammar"), as they failed to master "phase structure grammar" that requires understanding of hierarchical structures. Nonhuman primates are also able to combine calls in order to specify the meaning of an entire sequence for listeners (in putty-nosed monkeys, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2006; in wild Campbell's monkeys: Zuberbühler, 2003; in baboons: Bergman et al., 2003; in wild chimpanzees: Crockford & Boesch, 2005, in wild gibbons: Clarke, Reichard, & Zuberbühler, 2006). However, there is no evidence of hierarchical structure within the sequence of calls emitted. Thus, the use or comprehension of syntactic rules in nonhuman primates is not comparable to the mastery of embedded structures, a key characteristic of human language. Finally, although the use of symbols on a keyboard in communicative contexts has been demonstrated in linguistically trained great apes (e.g., Rumbaugh, 1977; Savage-Rumbaugh, Shanker, & Taylor, 1998), to our knowledge, there is no evidence of natural symbolization, a central trait of language, in nonhuman primates either in gestural or in vocal communication.

This chapter has pointed out that our primate cousins offer a remarkable source of information for investigating language origin. Given the current findings, we believe that the available studies on primate communication systems provide more robust arguments for the gestural hypothesis of language origin than the vocal hypothesis. However, there is still much to discover in the communicative behaviour of nonhuman primates. By using novel brain imaging techniques, we hope that future investigations of both vocal and gestural communication systems in nonhuman primates will clarify the continuities and discontinuities between us and our forebears and delineate more precisely the limits, if any, of human uniqueness.

ACKNOWLEDGEMENTS

NOTES

1 Imperative gestures are used to get another individual to assist in attaining a goal (Bates, 1976).
2 Declarative gestures are used to draw another's attention to an object or merely for the sake of sharing attention (Bates, 1976).
3 In humans the superior temporal gyrus (STG) is part of the temporal lobe of the brain and notably includes low-level auditory structures such as the primary auditory cortex (involved in the perception of sounds) and high-level structures such as Wernicke's area (involved in language processing).
4 In humans, the inferior frontal gyrus is part of the frontal lobe of the brain and notably includes Broca's area and neurons controlling muscles used for facial expressions in the primary motor cortex.

Part II

Cognition

4 Socioemotional factors in the development of joint attention in human and ape infants

Kim A. Bard and David A. Leavens

In this chapter we consider the idea that apes and humans share certain types of learning processes due to their shared evolutionary history. These learning processes begin early in life, rely on intersubjective, socioemotional factors, and are the backdrop for cognitively interesting outcomes like communicative gestures and joint attention. Moreover, they are the basis for the flexibility and plasticity observed in the early development of humans and apes.

WHAT IS JOINT ATTENTION?

Joint attention, is variously labeled shared attention (Adamson & Bakeman, 1991), a "meeting of minds" depending on "shared context and shared presuppositions" (Bruner, 1995, p. 6), a form of secondary intersubjectivity (reviewed in Trevarthen & Aitken, 2001), and triadic skill indicative of collaborative engagement depending on understanding of agency and of communicative intentionality (Tomasello & Carpenter, 2005).

Regardless of theoretical perspective, however, the operational (behavioural) definitions of joint attention show remarkably little variation across studies: Joint attention is when an individual is engaged with a social partner about an object or event. Engagement is typically defined as looking behaviour, and so joint engagement is defined as gaze alternation (looking at an object with interspersed glances at the social partner, or vice versa). Mundy and colleagues (Vaughan van Hecke et al., 2007) propose a useful tripartite consideration: *responding to joint attention* (RJA), which includes gaze following by the infant, and the following of points; *initiating joint attention* (IJA), which includes infant's pointing, showing, and gaze alternation; and *initiating behaviour regulation/requesting* (IBR), which functions to instrumentally manipulate a social partner to act on the world. Mundy et al. (2003) suggest that there is a distinction between the two types of joint attention (RJA and IJA) and requesting (IBR), as the former involve a social function, allegedly to share attention, whereas the latter, IBR, involves an instrumental purpose. Although behavioural performances are remarkably similar across studies, conclusions about underlying processes that support

the emergence, developmental sequalae, and thus the motivation for joint attention behaviours, differ dramatically across researchers.

THE COMPARATIVE AND DEVELOPMENTAL THEORETICAL PERSPECTIVES

As comparative psychologists, we compare specific aspects of behaviour across species (and across cultures) to understand evolutionary commonalities and distinctions of primate species' adaptations across evolutionary time. We focus on the primate lineage and in particular the hominoids. With this perspective, we can uncover species-unique characteristics (e.g., spoken language in humans), and shared characteristics (e.g., self-awareness). To uncover universals within a species, we need to compare across cultures, and to uncover species-unique characteristics we need to compare across species.

As developmental psychologists, we wish to understand the processes that explain how behavioural outcomes emerge in individuals of a species across their lifetime. Within this perspective, we are interested particularly in the infancy period. During early infancy, more so than later in life, we can more easily discern the interplay between nature and nurture that results in particular behavioural outcomes. We focus here on the interaction of emotion and cognition, and the influence of different social-cultural environments on this interaction (Bard et al., 2005).

Most often, however, we advocate the use of both perspectives. Asking both comparative questions and developmental questions at the same time, allows us to get closer to answering questions about commonalities and distinctions in developmental processes across primate species. We consider the changes in behaviour of individuals with age, comparing chimpanzees and humans explicitly at the same age, to better understand common developmental processes. For example, we studied the development of self-awareness from 15 to 30 months of age in human and chimpanzee infants (Bard, Todd, Bernier, Love, & Leavens, 2006). Additionally, with this combination approach, we specify those comparable learning conditions that support the development of a particular behavioural outcome, such as the referential problem space supporting production of pointing (Leavens, Hopkins, & Bard, 2005, 2008, and see later).

WHY STUDY JOINT ATTENTION IN CHIMPANZEES?

In humans, joint attention occurs around 9 to 12 months of age. Why should we expect that chimpanzees, our nearest living relatives, share this ability to coordinate attention to social partners with attention to objects?

Chimpanzee infants at birth are very similar to human newborns in neurobehavioural integrity (Bard, Platzman, Lester, & Suomi, 1992, 2001) and

reflexes (Bard, Hopkins, & Fort, 1990), and by 24–28 months are very similar in high-level sensorimotor cognition. Soon after birth, chimpanzee and human newborns are able to match facial actions of mouth opening and tongue protrusion of adult models (Bard & Russell, 1999; Meltzoff & Moore, 1977; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004), and newborn chimpanzees match a series of actions, including a tongue click sound (Bard, 2007). As newborns, both chimpanzees and humans appear quite comparable in their ability to imitate. But when we compare imitation abilities of older chimpanzees, then we find that chimpanzees have not performed very well, either in imitating arbitrary actions, imitating actions on objects, or imitating tool use (reviewed in Bard & Russell, 1999). In contrast, in their third year of life, chimpanzees show self-awareness through recognizing their mirror images (see Bard et al., 2006), a cognitive ability that human infants develop by 18 to 24 months of age. It is important to note that mirror self-recognition emerges in apes across a large diversity in specific rearing histories, including the entire spectrum of rearing histories identified by Call and Tomasello (1996), which includes chimpanzees raised in the wild, in laboratories and in human home-like environments (reviewed in Inoue-Nakamura, 2001). This is particularly interesting to comparative psychologists because mirror self-recognition is not found in any monkey species; it appears to be present only in the great apes and humans. Thus, self-recognition, in addition to many other cognitive skills typical of those which human infants develop by 18 to 24 months, are found in chimpanzees and other apes, but not found in monkeys, supporting conclusions about the comparability of sensorimotor cognition in humans and the great apes. These are good reasons to suspect that chimpanzees and humans might share other developmental outcomes in the first year of life, such as joint attention.

CAPACITY AND OUTCOMES

What do we mean when we say that humans are flexibly adaptive? Our combined developmental and comparative approach also allows us to better understand the evolutionary foundations for shared developmental processes, to understand epigenesis and variability in behavioural outcomes. Hare (2007) argued that "[o]ur species' unique flexibility of behavior, which is a product of our psychology, presents evolutionary theory with its biggest challenge" (p. 60). This challenge is being met with recent considerations of epigenetic processes, the complex interaction of nature with nurture (e.g., Garcia Coll, Bearer, & Lerner, 2004), and with specific focus on how variability emerges during development (a perspective called "evo-devo"; Michel, 2007). This new perspective highlights the contributions of four different routes of evolutionary change: genetic, epigenetic, behavioural, and symbolic. Epigenetic variations depend on the genotypic interactions with environment and the effects of these changes, the products of development

(Jablonka & Lamb, 2007). A compelling example is that cells of the liver, skin, and kidney, for instance, function differently, yet all are composed of the identical genetic information. Once the cells have become liver cells through their biological development, they continue to produce daughter liver cells. Behavioural inheritance is evident in rats' social and emotional regulation and in "transmission" of parenting styles across generations. And, for humans at least, a symbol-based inheritance (language) plays a substantial role in development and evolution. It is these nongenetic inheritance processes that support the variation that allows for adaptation to particular ecocultural environments while retaining a potential to adapt to alternative environments that results in the enormous variability across human cultures (Michel, 2007).

Gaskins (2006) argues that the three tenets of developmental psychology (specifically, that there are universal outcomes; that the long period of dependency in humans involves learning and therefore there is a large influence of experience on development; and that both the content and environment of learning are culturally organized and variable) cannot be held simultaneously, because the focus on universal outcomes tends to negate or downplay the variation attributable to learning and the influence of culture on experiences, learning, and outcomes. We agree with her proposed solutions: Mainstream developmental psychology must integrate cross-cultural knowledge, because development is learning dependent and variable, and many developmental outcomes are not universal.

We extend her solution with the inclusion of cross-species comparisons, which further support the identification of developmental processes for species-unique (or shared) capacities. For instance, all typically developing infants will learn a language, and many studies find infants have joint attention; therefore joint attentional competencies are hypothesized to link with the later emergence of language. Whether they are necessarily linked cannot be answered by studying the typical samples. However, with cross-cultural and cross-species comparisons, we can validate or refute this link. For instance, if similar early joint attentional outcomes exist in other species without the resulting emergence of language then we would conclude that joint attentional capacities are neither ontogenetically nor phylogenetically derived from our species-unique adaptations for speech and language (Leavens, 2004; Leavens, Hopkins, and Bard, 1996, 2005, 2008). Gaskins observes:

> [H]umans are not designed to be "Social" in general but to be "social" in a particular, culturally constrained way, just as they are not designed to learn "Language" in general, but one particular "language" . . . infants do not demonstrate "raw" expression of capacity but, rather an expression of capacity already heavily mediated by the specific socio-cultural environment.

(2006, p. 295)

We cannot measure the capacities of a species with the study of a single group in a single environmental niche. In developmental psychology, we typically study how a limited number of individuals develop within a particular ecocultural setting. The study of capacity requires multiple group comparisons. Moreover, the study of capacity relies on comparing variation in outcomes as a result of different developmental variables. Cross-cultural psychologists compare outcomes across ecocultural settings, whereas cross-species psychologists compare outcomes across species (representatives of which develop within particular settings). The effect of particular settings on development, in the human species, can be seen even within the first weeks of life (e.g., Bard, 2005), and in many social, emotional, and interaction outcomes by 3 months (e.g., mutual gaze reviewed in Bard et al., 2005; colicky crying, Bard, 2000). We suggest that to understand the capacity of chimpanzees as a species, we need to similarly consider variations in outcomes that occur across all learning settings.

HOW DOES JOINT ATTENTION DEVELOP?

Regardless of theoretical perspective, most studies find that typically developing human infants begin to display joint attention from 9 to 10 months of age (e.g., Adamson & Bakeman, 1991). Most perspectives assume that joint attention depends on both person engagement and object engagement since it emerges developmentally subsequent to engagement with caregivers (about 3 months) and subsequent to engagement with objects (emerges at about 5–6 months). Typically developing human infants display primary engagements with caregivers in face-to-face interactions with cycles of mutual gaze in an emotionally positive exchange. Typically developing human infants, from 5 to 6 months, engage in object play and increasingly complex manipulation. At 9–10 months these two strands of development appear to converge, and typically developing infants begin to engage in triadic interactions in regularly occurring routines of requesting and referring with caregivers about objects or events. Infants begin to respond to bids for joint attention, such as adult pointing, and also to initiate joint attention with showing, offering, pointing, and requesting.

Intersubjectivity appears to be a necessary precondition for joint attention. We find that intersubjectivity is a characteristic shared by chimpanzee infants and human infants (Bard, 2005) when definitions are based on behavioural criteria (Susswein & Racine, 2008), e.g., neonatal imitation; they engage in social games with mutual gaze (play dyadically). In some non-Western settings, primary intersubjectivity is expressed through tactile modalities and motoric stimulation, whereas in many industrialized settings, primary intersubjectivity is expressed through the visual modality and mutual gaze (Keller et al., 2004). Both of these human patterns of engagement with caregivers are also found in chimpanzee infants' engagement with caregivers (e.g., Bard et al., 2005).

WHAT IS "TYPICAL DEVELOPMENT"?

The scientific study of the socioemotional development of human infants bloomed in the 1960s. By 1975 we knew that infants had capacities for face-to-face interpersonal engagement (with neonatal imitation, mutual enjoyment, mutual gaze, and preverbal communicative turn-taking) that preceded developmentally their rich involvement with objects (that we knew well through Piaget's, 1952, documentation of sensorimotor cognition). In fact, we were also beginning to learn about the ways in which culture influences early development (e.g., Bullowa, 1979) and about alternate pathways in development (reviewed in Greenfield, Keller, Fuligni, & Maynard, 2003). With the traditions of Piaget and behaviourism, developmental psychologists were looking for human universals, especially in terms of developmental outcomes.

Moreover, findings from middle-class industrialized cultures, depicted as the Euro-American norm, were assumed to describe species-typical "typical developmental outcomes". While developmental psychologists of the 1970s were highlighting Vygotsky's notion of the co-construction of knowledge by caregiver and infant, they were also advocating the universality of developmental outcomes. Only recently have developmental psychologists embraced culturally specific developmental outcomes (e.g., Greenfield et al., 2003; Keller et al., 2004; Rogoff et al., 1993). Any scientific characterization of typical development must include those variations in developmental outcomes, developmental trajectories, and adaptive interactions with cultural environment that are found across different groups of humans. In terms of joint attention, for example, studies from Euro-American perspective emphasized the first triadic engagements, whereas studies from more traditional and interdependent societies focus on how the infant develops multiplicity of attention, "attend[s] to several events simultaneously (such as working an object with the caregiver and monitoring other conversation, glancing at and being involved with the flow of events)" (Rogoff et al., 1993, p. 85).

A similar argument must be made for the importance of looking at variations in developmental outcomes, trajectories, and adaptive interactions with the environment when studying chimpanzees. Chimpanzees, as a species, share with humans, as a species, responsiveness to environmental, cultural, and socioemotional factors during development. There is not a single developmental pathway for the chimpanzee species. These learning processes begin early in life, rely on intersubjective, socioemotional factors, and are the backdrop for cognitively interesting outcomes like communicative gestures and joint attention. These learning processes provide the basis for the flexibility and plasticity observed in the early development of humans and apes.

EXPERIMENTAL STUDY OF THE INFLUENCE OF
SOCIALIZATION ON JOINT ATTENTION
IN CHIMPANZEES

Bard and Gardner (1996) conducted a study focusing on the first year of life, beginning at 3 months when infants first learn about objects through to 12 months, when infants have developed the ability to coordinate attention toward social agents, with attention to actions on objects. The specific aim was to explore the impact of differential socialization on the development of cognitive skills, such as joint attention. Here we briefly consider the links between attention, cognition, and emotion that are apparent early in life. Most importantly, we consider the effects of socialization on attention, cognition, and social-emotional systems.

Fifteen chimpanzees were given Standard nursery rearing at the Yerkes Center, which emphasized the value of peers as social companions. In the first month of life these infants spent the majority of their time in a heated incubator, but were given bottles and diaper changes by caregiving staff on a scheduled basis. Small groups of same-aged individuals were formed as early as 6 weeks of age. By 1 year of age, these peer groups were playing together in outdoor enclosures during the daytime, and sleeping together in double cages at night. A few times each day, caregivers might spend up to an hour playing with the group. There were about three caregivers for the entire nursery of 20 to 25 chimpanzees, resulting in a ratio of about one caregiver to 8 infants. Standard Care was designed with the philosophy that the chimpanzees would learn how to be competent primarily from their same-aged peers.

Seventeen chimpanzees were given Responsive Care (Bard, 1996). Responsive caregiving consisted of 4 hours per day, 5 days per week, of continuous physical contact with specially trained human caregivers from birth through 1 year of age. Responsive Care was designed to provide care that more closely approximated chimpanzee species-typical care than that of standard rearing. In general, the Responsive Care project was designed to provide not only for the physical needs of the chimpanzees, but to provide for their emotional needs, as well. There was most often a 1:1 caregiver, infant ratio, but occasionally one caregiver provided responsive care to two chimpanzee infants at a time. Responsive Care was designed with the goal to facilitate the development of each chimpanzee's coping skills—so that rather than becoming dependent on us they would learn to depend on their own skills.

Responsive care was enriching, nurturing communicative skills that standard care did not (Bard et al., under review). Here the major comparison is with a third group, those chimpanzees that experienced very early stress and late arrival in the nursery. A small group of infants initially remained with their biological mothers, but were brought to the nursery before they were 3 months old and then received standard care; this is the Early Stress group. The mothers had "marginal maternal competence", which means that although they had sufficient maternal behaviours for the infant to survive

initially (that is, they cradled their infants and allowed the infants to nurse), they didn't have sufficient maternal care for the infant to remain with them past the first weeks of life (see Bard, 1994, for more details of marginal versus good maternal competence in chimpanzees). Every effort was made to have every infant remain with its mother, so these infants could be quite stressed (physiologically and behaviourally) by the time they were removed from her marginally competent care. There were five chimpanzees that spent less than 25 days with their mother and were then given standard nursery care.

Cognitive development was measured for all nursery-reared chimpanzees with the Bayley Scales of Infant Development (either called the Bayley or the BSID; Bayley, 1969), the most commonly used standardized test for human children from 3 months to 3 years of age, measuring cognition (Mental Development Index or MDI). We were particularly interested in factors from the Infant Behaviour Record: Task—a measure of meeting the demands of the test; Affect—a measure of social and emotional responses; Activity—a measure of body movement; and Reactivity—a general measure of sensitivity to sights and sounds (Bard & Gardner, 1996). Thus, we could assess the effects of socialization on each of these factors which contribute to performance on the joint attention tasks typically passed by 9-month-old human infants.

At 9 months, there was significant group difference in cognition: The Responsive Care infants were significantly better than the Standard Care infants; the standard care infants were about the same as the human norm, and the early stressed chimpanzees were significantly worse. Cognition was strongly and significantly related to socioemotional scores ($r = .84$, $p < .001$), and motivation ($r = .55$, $p < .001$).

The experience of severe stress in the first weeks of life appeared to have a detrimental effect on attention, in the form of significant decreases in the attention span (duration of attention), and in goal-directedness at 9 months of age. There was no difference between responsive care and standard care groups, suggesting that enrichment does not enhance attention span. Early rearing had an impact on activity and reactivity—two aspects of infants that are typically thought to be inborn and stable individual differences. Early stress had detrimental effects on levels of activity and changed the developmental pattern of reactivity. Enrichment, on the other hand, only seemed to have positive effects on muscle tone, resulting in significantly more relaxation through the first year of life.

There were very strong effects of socialization on social and emotional responsiveness. This factor includes assessments of each chimpanzee's general emotional tone, social orientation, and responsiveness, both to the examiner and to the mother, cooperation with the examiner, and fearfulness. Responsive Care infants were the happiest and least fearful in emotional tone, and the early stress group were the least happy and most fearful. There were different developmental trajectories for each group, the standard care infants remained content from 3 to 12 months. Enrichment increased the levels of happiness

and decreased fearfulness, and the effect was linear from 3 to 12 months (see Bard & Gardner, 1996, Fig. 11.3). Early stress, in contrast, caused a peak in fearfulness at 6 months, and a dip from content to unhappy at 6 months, with a return to the level of standard care by 12 months.

A similar pattern of developmental trajectories was evident in social cooperation with the examiner and her requests. Standard Care infants were accepting of the examiner's requests. But Responsive Care infants improved from accepting at 3 months, to enjoying the give and take of objects by 12 months. Early Stress individuals were accepting at 3 months, but then were more often rated as refusing to cooperate at 6 months, and were significantly less cooperative than the Responsive Care infants at 12 months. It is important to note that these differences were not a result of differences in bonding with the favourite caregiver, because all groups exhibited equal levels of social responsiveness to their favourite caregiver, who acted as a mother surrogate in these tests.

In summary, we found that early rearing experiences influence the development of cognition, by acting differentially on task-related aspects of performance, on temperamental variables, on emotional responsiveness, and most importantly on social cooperation. The experience of severe stress in the first month of life had lingering detrimental effects on outcomes throughout the first year of life, whereas enriching laboratory care had positive effects especially on emotional responsivity and social cooperation.

DOES JOINT ATTENTION OCCUR IN CHIMPANZEES?

Joint attention, broadly defined as the ability to coordinate attention towards social agents with attention to objects, has been found in chimpanzees across many settings. This coordination of object attention with attention to social agents is found, for instance, in infant chimpanzees from about 9 months, when they beg for food from their mothers with the use of gesture (van Lawick-Goodall, 1968). Bard (1992) argued that intentionally communicative gestures, like the hand held palm up at the mother's mouth while she is eating, awaiting the gifting of pieces of food, can be viewed as tertiary circular reactions in Piagetian cognitive terms (see Bard, 1990, for more extended discussions of this social form of tool use).

From as young as 14 months, chimpanzees engaged in social referencing, alternating their gaze from favourite caregiver to novel objects at a rate identical to that found in human infants tested in similar conditions (Russell, Bard, & Adamson, 1997). In the wild, social referencing occurs as well, but since eye gaze is difficult to see (and is sometimes not congruent with head direction: Bethell, Vick, & Bard, 2007), especially under field conditions, social referencing has been underreported (van Lawick-Goodall, 1968).

POINTING

By 5 years of age, chimpanzees in a laboratory situation reliably initiate joint attention with experimenters about food items, through pointing and other communicative signals (e.g., Leavens & Hopkins, 1998). Chimpanzees and other apes who are faced with unreachable, but desirable food, will typically gesture towards either the food or a human experimenter while alternating their gaze between the food and the experimenter (Leavens & Hopkins, 1998; Leavens, Hopkins, & Thomas, 2004; Woodruff & Premack, 1979). Apes will also point towards tools that are necessary for retrieval of food that has been, for example, locked in a crate (e.g., Call & Tomasello, 1994; Russell et al., 2005; Whiten, 2000). There is substantial variability in the relative incidence of pointing among great apes: Wild apes virtually never point (for an exception see Veà & Sabater-Pi, 1998), about half of the apes raised in laboratory environments point, and virtually all language-trained or home-raised apes point (Call & Tomasello, 1996; Leavens, Hopkins, & Bard, 2007). Moreover, with respect to preferred pointing posture, laboratory-reared apes prefer to point with their whole hands, whereas language-trained apes prefer to point with their index fingers (Leavens & Hopkins, 1999). This kind of pointing, to request delivery of otherwise unreachable food, is commonplace in captivity and an example of IBR—requesting that a human act on the world.

Tomasello and Carpenter wrote:

> [T]here does not seem to be anything in chimpanzee ontogeny comparable with the human developmental pathway for sharing and collaborating with others, that is, for engaging with others in protoconversations, declarative communication, and complex collaborative activities involving joint intentions and attention.
>
> (2005, p. 113)

This statement neglects a body of research in which chimpanzees engage in actual conversations, declarative communication, and complex collaborative activities, specifically the numerous long-term ape studies (Gardner & Gardner, 1971; Hayes & Hayes, 1954; Kellogg & Kellogg, 1933; Premack, 1976; Rumbaugh, 1977; Savage-Rumbaugh, 1986). Why have these studies been so collectively ignored or even dismissed in considerations of the capacity of the chimpanzee species?

For present purposes, it is sufficient to note that these cross-species language studies report that their subjects display the complete triad of joint attentional competencies outlined by Mundy and his colleagues: RJA, IJA, and IBR. To argue, as Tomasello and Carpenter argue, that chimpanzee ontogeny is not comparable with human developmental pathways is to claim that (a) there is a single typical human developmental pathway, which we know to be false, (b) we should ignore every experimentally cross-fostered chimpanzee raised by humans, despite the fact that human development is

critically dependent upon being raised by humans, and (c) we should only compare the behaviour of wild apes raised in "natural" circumstances with humans who are raised in patently artificial circumstances. Implicit in this view is the idea that humans develop joint attentional competencies because of species-specific cognitive and motivational adaptations unique to the human lineage. A priori, then, Tomasello and Carpenter (2005) reject a large body of evidence that strongly suggests that humans and apes will learn joint attentional competencies in similar caregiving environments. When they conclude that "Our hypothesis is that the chimpanzees do not understand the communicative intentions behind the pointing gesture . . . precisely because they have not constructed with their partner such a shared joint attentional format" (p. 110), they emphasize hypothetical deficiencies in the chimpanzees, rather than deficiencies in the caregiving environments. We argue that because almost every ape ever exposed to intensive, daily, affect-laden interactions with humans develops the abilities to follow points and gaze and to produce pointing, therefore, these joint attentional competencies are elicited by some caregiving contexts in *both* humans and apes. Thus, we are in agreement with Carpenter, Tomasello, and Savage-Rumbaugh (1995) when they wrote that "a human-like sociocultural environment is an essential component in the development of human-like social-cognitive and joint attentional skills for chimpanzees, and perhaps for human beings as well" (p. 217).

It is worth noting that humans who develop joint attentional competencies take many months to acquire these skills (e.g., Adamson, 1996), yet few researchers take seriously the idea that these many months of experience might be relevant to the development of joint attention (for exceptions, see Moore & Corkum, 1994; Susswein & Racine, 2008). Nobody would reasonably expect a year-old human baby who was raised in a cage without a primary adult caregiver to suddenly display complete mastery of joint attentional routines if they were pulled out of that environment for a few days' worth of experimental trials, yet this is precisely what is expected of many captive-reared apes (Leavens, 2006; Leavens et al., 2008). If joint attention is a developmental outcome that takes many months to become manifest, then we argue that it makes more sense to examine the developmental precursors to this skill than it does to invoke a human species-specific cognitive adaptation, particularly in light of the comparative data that show that the more humanlike the rearing environment of apes, the more the apes act like humans.

There is a central concern in contemporary comparative and developmental psychology with an apparent difference between humans and apes in the use of IJA; many researchers have noted that apes will display pointing in IBR contexts, manipulating the behaviour of their human companions, but not in IJA contexts, in which establishing joint attention is apparently performed towards the end of mutual contemplation or appreciation of some distant object, location, event, or animate being (e.g., Tomasello, 2006; Tomasello & Camaioni, 1997; Vauclair, 2004). We have discussed this issue at length elsewhere (Leavens, 2004; Leavens et al., 2008; Leavens, Russell, &

Hopkins, 2005). In short, because apes in captivity spontaneously develop referential strategies to request otherwise unattainable goals, we argue that their apparent reluctance to point in contexts of sharing attention to distant events cannot be due to a primary cognitive deficiency, relative to humans, because all of the behavioural elements for triadic communication are fully manifest in these kinds of contexts. Apes point to objects, alternate their gaze between humans and these distant objects, and display context-appropriate selection of communicative signals in different sensory modalities, communicating with visual signals when a human is attentive and switching to auditory signals when a human is inattentive (e.g., Hostetter et al., 2001; Leavens & Hopkins, 1998; Leavens, Hostetter, et al., 2004; Leavens, Hopkins, & Thomas, 2004). Thus, because these mechanical elements of triadic communication spontaneously arise in captive ape populations in the absence of any explicit training, apparent differences between humans and apes in their propensity to engage in IJA are therefore attributable to motivational, rather than cognitive factors. Pointing in IBR contexts therefore constitutes evidence for instrumental use of pointing towards the goal of object delivery, whereas pointing in IJA contexts is evidence for the similarly instrumental use of pointing towards the different goal of sharing attention (e.g., Leavens, 2004; Leavens, Hopkins, & Bard, 2005). The question is, does this apparent motivational difference between apes and humans indicate a difference in ontogenies or in phylogenies?

In accordance with the striking and long-lasting effects of early rearing history experiences in infant chimpanzee social development, discussed earlier, we argue that only when apes are raised in socioemotional circumstances identical to those experienced by typically developing Western human children can any reasonable conclusion be drawn. Although numerous apes have been raised in ordinary human family circumstances, few of these apes are described in the scientific literature. To our knowledge, only five apes have been raised from birth throughout childhood by stable, loving, human foster parents who published their observations in the scientific literature: Vicki, who was raised from a neonate to a 7-year-old by Hayes and Hayes (1954), Moja, Tatu, and Dar, who were raised by Gardner and Gardner (1989) from 1 to 5 days after birth to 5 years of age, and Lucy, who was raised from birth through adolescence by Temerlin (1975). These latter apes, like many language-trained apes, have been reported to display many instances of apparent IJA. Thus, when apes are raised by humans in circumstances that approach this kind of richly emotional and responsive caregiving quality, then we find that these apes occasionally exhibit something like IJA (although, contrary to the argument we're making here, Vicki apparently did not: Hayes and Nissen report that "none of Vicki's gestures conveyed anything but requests", 1971, p. 107; however, many of her imitations involved RJA; Hayes, 1952). But because cross-fostered apes are more typically cross-fostered by humans long after the neonatal period, it is ambiguous whether apparent differences in propensity for IJA are attributable to species or

developmental differences. We suspect that there may be systematic differences in motivation between apes and humans (cf. Tomasello, 2006), but we are arguing here that the evidence available cannot adequately speak to the question.

THE REFERENTIAL PROBLEM SPACE

Pointing thus reflects a cognitive capacity that is shared by humans and apes, irrespective of the specific motivation to display that pointing. It has been repeatedly noted that apes in the wild do not point and there is a widespread fallacious argument to the effect that because wild apes do not point, therefore, there is a species difference in cognition between apes and humans (e.g., Povinelli, Bering, & Giambrone, 2003; Tomasello, 2006). This argument is based on an assumption that because the gestural communication of wild apes is displayed in natural contexts to which these animals are adapted by natural selection, the communicative repertoires of wild apes are more "natural" than those of captive apes, who are "contaminated" by human contact. This assumption completely misses the very obvious point that contemporary humans, from whom all of our norms for typical communicative development are derived, are raised in profoundly novel rearing circumstances, utterly unprecedented in many key respects. It is not reasonable to suggest that pointing by human babies is "natural" when it is displayed by children raised in artificial urban or suburban environments to which they are obviously not adapted by natural selection. We, therefore, reject this argument and emphasize the *similarities* in the systematic sociophysical circumstances in which humans and captive apes point (Leavens, Hopkins, & Bard, 2005).

Like human babies, captive apes cannot directly reach items of interest. Human babies spend substantial portions of their early lives in situations of restraint: in cribs, high-chairs, cots, backpacks, car seats, etc. Human babies are also relatively immobile due to endogenous limitations on their rates of motoric development. Captive apes are also perpetually restrained by cage mesh or bars. Human babies have long-established histories of food and object retrieval by their human caregivers. Captive apes often never consume a single calorie in their decades-long lives that hasn't been delivered by their human caregivers. Faced, thus, with a desirable, but unreachable object in proximity to a caregiver with an established history of object delivery, both human infants and captive chimpanzees face a problem in coordinating the activity of the human caregiver in relation to the unreachable food. This is the Referential Problem Space and pointing emerges as a solution to this problem in both human infants and captive apes (Leavens et al., 1996, 2008; Leavens, Hopkins, & Bard, 2005). The cognitive implication of pointing in these contexts is simply that both apes and humans can exercise means–ends reasoning to solve a common problem faced in their daily lives (e.g., Bard,

1990, 1992; Bates, O'Connell, & Shore, 1987). This explanatory framework has the great strength that it can easily account for why wild apes never or only very seldom point: Because they are never restrained and because they achieve competent independent locomotion well in advance of developing means–ends reasoning skills, they are never dependent upon others to act on the world for them, and therefore developmental trajectories in the wild completely bypass the Referential Problem Space (Leavens, Hopkins, & Bard, 2005).

This appeal to specific sociophysical circumstances constitutes an argument to the effect that both humans and apes will adopt similar communicative behaviours in similar rearing circumstances. Like pointing, the display of mutual gaze between mother and infant was long incorrectly maintained to be a human species-unique behaviour. In what follows, we generalize the epigenetic argument of the origins of pointing to the emergence of mutual gaze in humans and apes.

MUTUAL GAZE (INTERPERSONAL ENGAGEMENT)

Mutual engagement with caregivers is evident in face-to-face positive inter-actions with mutual gaze and social smiles, which emerges in most human infants, from 6 to 8 weeks of age. Developmental psychologists consider mutual gaze important, because it reflects the initial emotional bond, it may set the stage for human unique learning (e.g., language), and it is the early context in which the function of eye gaze can be studied. Interestingly, there is wide variation across cultures in the prevalence of mutual gaze, as many interdependent cultures preferentially value close physical contact (see Keller et al., 2004), whereas most industrialized cultures value independence and more distal visual engagement.

> The sort of intimate face-to-face mother–infant interaction that has been the subject of much developmental research may be very atypical in cultural settings where infants are less oriented toward their parents as primary social partners and instead function as members of the community with less individual, dyadic focus.
>
> (Rogoff et al., 1993, p. 15)

Goals of development vary across human cultures, with differences in the involvement of children in adult activities, and the role of adults in socialization. Rogoff emphasizes the role of learning through (nonparticipant) observation in many cultures, where children are responsible for learning. This raises questions about the assumption that caregivers must also function as teachers in order for human learning to occur (see Gaskins, 2006).

Our study of mutual gaze in chimpanzee infants illustrates that variation also exists across chimpanzee groups. In some chimpanzee groups positive face-to-face interactions emerge from 6 to 8 weeks of age, whereas in other

groups, close physical contact is the preferred modality for mutual engagement (Bard et al., 2005).

Eye gaze patterns, such as mutual gaze at 3 months, may provide a foundation for later understanding of eye gaze, in chimpanzees as in humans (Tomasello, 1999; Tomonaga et al., 2004). In humans the social functions of eye gaze develop beyond those evident in the dyad (Trevarthen & Aitken, 2001), to those that involve a triad of the infant, social partner, and object (i.e., joint attention). Can "higher" functions of gaze develop in the absence of high levels of mutual gaze? Surely, it must be the case that these more complex functions of eye gaze do develop in other human cultures—perhaps the Western focus on the referential triangle (parent and infant and OBJECTS) is too simplistic. Perhaps, as Rogoff et al. (1993) suggested, a toddler in the Mayan setting has developed an ability to attend simultaneously to multiple tasks—attending to the mother, to a younger sibling, to the social group, their own activities with objects, their mother's activity with different objects, and the social groups' activity as well. Possibly, this simultaneous focus on multiple events may be profitably explored across species as well as across cultures. Clearly the focus on defining joint attention as merely triadic does not fully capture the human range of attentional foci evident in children across cultures (Rogoff et al., 1993; see Fivaz-Depeursinge & Corboz-Warnery, 1999; Reddy, 2003).

CONCLUSIONS

In this chapter we have made the following specific claims:

1   Ape and human development is very sensitive and responsive to early differential rearing experiences, even very early, in the first days of life.
2   These early responses to the environment have effects on sociocognitive development, and sociocognitive outcomes, including joint attention.
3   A range of joint attentional behaviour is displayed very commonly by captive apes in the absence of overt training.
4   Joint attentional competence in captive apes is variable and related to early developmental experiences.
5   Pointing is a manifestation of sensorimotor cognition in both humans and apes.
6   Apes in the wild bypass the Referential Problem Space and so pointing per se does not develop.
7   Like pointing, the propensity for mothers and infants to engage in mutual gaze is dependent upon specific socioemotional—cultural circumstances of the rearing environment.

These considerations lead us to the view that apes can be valuable models for the development of numerous human developmental features that have been

heretofore labelled as emerging uniquely within our own lineage. We think that we have a great deal to learn from animals about human development.

ACKNOWLEDGEMENTS

5   Collective intentionality and the roots of human societal life

Hannes Rakoczy

What can we learn from animals? In this chapter, I would like to pursue the more specific question: What can we learn from other animals about what kind of social animals we are, and how we become so? Obviously, human sociality is quite unique. Our cooperative, societal, and institutional forms of life clearly set us apart from the rest of the animal kingdom. From an onto-genetic point of view, I will inquire into the potential cognitive underpinnings of such unique sociality and its development. The ontogeny of different forms of intentionality in early childhood will be traced, with a comparative eye on common primate and uniquely human aspects. The picture that emerges will be this: We share with other animals, in particular great apes, basic forms of individual intentionality, and probably even simple forms of individual second-order intentionality that develop in human ontogeny in the course of the first one and a half years. What lies at the heart of uniquely human cognition, though, and what lays the foundation for uniquely human sociality, is the ability to enter into collective "WE"-intentionality, which develops from the second year on.

INDIVIDUAL INTENTIONALITY

Intentionality in the broad philosophical sense of "aboutness" is the mark of the mental (Brentano, 1874/1973; Dennett & Haugeland, 1987; Searle, 1983). To be capable of mentality is to be able to entertain intentional, contentful attitudes (beliefs, desires, intentions, etc.) towards the world and to be guided by these in reasoning and rational action.

A central assumption in the Cartesian tradition was that there was a fundamental divide between different kinds of creatures that explains the radical differences between their forms of life: On the one hand, there were humans with their monopoly on intentionality, which enabled them to speak languages and live in culture and societies. And on the other, there were the rest of the animals—mere soulless automata, brutes without culture.

Needless to say, this simple picture is not taken seriously any more. Without Cartesian ontological substance dualism, all animals—humans

included—are physical beings and thus automata at some (physical) level of description. But on another, folk psychological level of description, humans are correctly characterized in intentional terms—and so are some other animals, as they display systematic and differentiated behaviour that from a folk psychological standpoint or an "intentional stance" (Dennett, 1987) provides grounds for ascribing at least simple forms of intentionality (see Bermudez, 2003; Hurley, 2003).

Let me mention two relevant examples from a developmental psychological perspective that help to bring out the analogy between the intentionality developed early in human ontogeny and intentionality in other species, namely object cognition, and planned action. In developmental psychology since Piaget's (1952) seminal work, thinking about an objective world—in its simplest form: thinking about objects existing as "out there"—and acting intentionally and in planned ways have been stressed as the two major milestones in the transition from purely sensorimotor dealings with the world to intentionality proper. All thinking requires a minimal notion of objectivity: The objects thought about exist independently from the perceiver and enduringly out there in the world. Regarding human ontogeny, Piaget has described infants' development from initial undifferentiated sensation without any notion of persisting objects ("out of sight, out of mind") to what he called "object permanence"—the appreciation that objects continue existing objectively whether perceived or not. In their actions infants begin to display object permanence from (at latest) the end of their first year; they begin to search for occluded and hidden objects they previously perceived. Furthermore, infants from around 1 year not only track objects as chunks of matter continuously existing in space and time; they also individuate objects as objects of certain kinds, e.g., this chair, that table, that rabbit. Recent findings suggest that by 1 year of age infants begin to apply our common sense metaphysical framework of objects as enduring substances, individuated under sortal (kind) concepts—and thus share the rudiments of our adult conceptual architecture of objective thought (van de Walle, Carey, & Prevor, 2000; Xu & Baker, 2005; Xu & Carey, 1996).

Many other animals are on a par with infants; many primate species, and dogs, for example, reach the highest levels of Piagetian object permanence, levels typically reached by infants in the second year (reviewed in Tomasello & Call, 1997). Recent research suggests that some monkeys and great apes also individuate objects qua objects of certain kinds much in the same ways as human 1-year-olds do (Mendes, Rakoczy, & Call, 2008; Phillips & Santos, 2007; Santos, Sulkowski, Spaepen, & Hauser, 2002).

The second milestone in the development of intentionality in human ontogeny stressed by Piaget is the emergence of intentional, planned action. While much behaviour may be voluntary right from the start, the first clear instances of intentional instrumental action, i.e., actions done purposefully and in a planned way in order to achieve some end in mind, appears in human ontogeny towards the end of the first year: Infants organize their behaviour in

means–ends structures and indicate an awareness of the relations between means and ends. In a classic example, infants remove barriers in order to reach a desired object or pull a cloth, on which a desired object is placed, towards them in order to be able to grasp it. And they persist until they achieve their end, varying their means if necessary (Piaget, 1952; Willats, 1985, 1999). These phenomena are also widespread in the nonhuman animal kingdom. Many species, notably primates, show instrumental problem-solving of remarkable complexity—Köhler's (1926) apes perhaps being the most famous examples.

In sum, many animals share with us the bare bones of simple individual intentionality.[1] Like human infants from around 1, many animals are capable of the most basic form of objective thought: perceiving and cognizing about objects. And many animals don't just behave, but perform intentional instrumental acts in planned ways. Not to mention the remarkable cognitive abilities recent research has found in many species concerning, for example, causal reasoning, self-recognition, tools use, memory, simple numerical cognition, etc.

SECOND-ORDER INTENTIONALITY

Whatever it is that explains the uniqueness of human cultural, linguistic, and societal life forms in contrast to all other species' forms of life, it cannot be that humans have intentionality, while other animals lack intentionality of any kind. So what is the crucial dividing line? One prominent candidate in comparative research in the last decades was not individual intentionality as such, but the ability to understand others and oneself qua intentional beings— second-order intentionality, also called "theory of mind" after Premack and Woodruff's seminal paper "Does the Chimpanzee have a Theory of Mind?" (1978). So-called "theory of mind" research became a booming field in developmental and comparative psychology when philosophers and psychologists joined efforts to find suitable operationalizations of second-order intentionality (Bennett, 1978; Dennett, 1978; Harman, 1978; Wimmer & Perner, 1983). The ability to ascribe epistemic subjectivity to others and to oneself in the past, i.e., to attribute intentional attitudes that represent reality as being a certain way—which aim at truth but may be false (paradigmatically, false beliefs), emerged as the accepted milestone for full-fledged second-order intentionality. Empirically, it turned out that around 4 years of age in human ontogeny a social-cognitive "revolution" occurs; children begin to manifest a suite of new behaviours. They ascribe false beliefs to others (and themselves in the past) and explain and predict their actions accordingly (see Wellman, Cross, & Watson, 2001, for a meta-analysis). They distinguish appearances from reality (Flavell, Flavell, & Green, 1987) as well as the different observers' conflicting perspectives on the same situation (Flavell, Flavell, Green, & Wilcox, 1981; Perner, 1991). And they begin to intentionally deceive others, i.e., lead them to have false beliefs (Sodian, 1991).

Clearly, second-order intentionality of this kind is crucial to many characteristically human activities and achievements such as self-consciousness and reflective thinking, full-fledged communication (on Gricean analyses), and complex conventional activities (Lewis, 1969). And it seems quite clear and with (almost) consensus in the field that no other species, not even chimpanzees, attain these sophisticated levels of second-order intentionality (see, e.g., Call & Tomasello, 1999).

Soon, however, simpler forms of second-order intentionality like understanding perception and intention received attention, shifting the focus from full-fledged epistemic subjectivity (in particular, false beliefs) to simpler intentional attitudes. Recourse to John R. Searle's taxonomy of intentionality might help to clarify this issue. Searle (1983), following Anscombe (1957), distinguishes two kinds of intentional attitudes that have close analogues in different kinds of speech acts. First, there are cognitive attitudes with "mind-to-world" direction of fit. Their job is to bring the mind in accordance with the world. Beliefs and knowledge are the paradigm cases, but perception falls into this category as well. Second, there are conative or "pro" attitudes (Davidson, 1963) with "world-to-mind" direction of fit whose job is to bring the world into line with the content of the attitude, e.g., desires, wishes, hopes, and intentions. Now, while beliefs and desires are the paradigm cases on both sides, there are specific attitudes on each side on the "periphery" towards the world that, according to Searle, are the biologically and ontogenetically primary ones: perception (on the mind-to-world side) and intentions (on the world-to-mind side).

What came into focus was the following possibility: Just as the first intentional attitudes that develop in human infants and other animals concern perception (of an objective world) and intentional action, the first form of second-order intentionality to develop should be an understanding of perception and action. And with this arose the further possibility that the divide between humans and other animals might go, ontogenetically speaking, even deeper. It might be that while the development of simple individual intentionality in humans and nonhuman primates runs in parallel, humans surpass all other animals in developing even simple forms of second-order intentionality.

The development of simple forms of second-order intentionality in human infancy has been described as the "9-month-revolution" in analogy to the social-cognitive revolution at 4 years (Tomasello, 1995b, 1999). This cognitive revolution in social understanding manifests itself in several distinct—but cognitively related—behaviours that first emerge around this time: After engaging in "dyadic" behaviours with either persons or objects for some time during the first year, children for the first time begin to engage in "triadic" behaviours that involve a referential triangle between child, another person, and an object/event that is jointly perceived/attended to or acted upon. Infants at this age begin to flexibly and reliably look where adults are looking (gaze following), understand what others do and don't see

(perceptual perspective taking), use adults as social reference points to disambiguate novel events (social referencing), and act on objects in the way they have seen adults act on them (imitative learning)—revealing an understanding of the adults' attitude/directedness towards the outside events (reviewed in Carpendale & Lewis, 2006; Carpenter, Nagell, & Tomasello, 1998; Tomasello, Carpenter, Call, Behne, & Moll, 2005). At the same age, infants also begin to use communicative gestures like pointing to direct adult attention and behaviour to entities and make protocomments on them (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004), trying to influence the adult's attitude/directedness towards the events (Tomasello, 1995b). The fact that all these skills emerge in developmental synchrony and a correlated fashion (Carpenter et al., 1998) suggests a common underlying cognitive basis—an emerging understanding of oneself and others as intentional agents.

The importance of these cognitive abilities for developing cultural and linguistic forms of life is obvious. Learning a language presupposes a rudimentary notion of other speakers' perceptual perspectives and a rudimentary understanding of what they are up to. And cultural development essentially involves imitation as a form of reliably reproducing what one takes others to do intentionally.

Even great apes do not naturally and spontaneously point out things to one another (Povinelli & O'Neill, 2000) nor do they imitate each other (Tomasello, 1996). And most studies during the 1980s and 1990s failed to find convincing evidence for perceptual perspective taking (Povinelli & Eddy, 1996) or any other kind of social-cognitive abilities present in infants after the 9-month-revolution (reviewed in Povinelli & O'Neill, 2000; Tomasello & Call, 1997). Thus, one proposal became widely accepted in the field: The roots of uniquely human life forms lie in even the simplest forms of second-order intentionality that human infants develop early in ontogeny, but which no other species develops (e.g., Povinelli & Prince, 1998; Tomasello, 1999). These forms of social understanding enable humans to acquire language and to enter into culture, and their absence in other species explains why they do not develop cultural forms of life.

This simple picture, however, has been called into question by recent research, which suggests that chimpanzees might also be capable of at least simple second-order intentionality. First, a series of studies by Hare et al. (2000) and Hare et al. (2001) found that chimps understand something about others' perception. In a food competition situation, a subordinate and a dominant chimpanzee were placed in separate rooms on opposite sides of a third room. In the crucial conditions, food was placed in the third room so that the subordinate could see two pieces of food hidden while the dominant only saw one (his line of sight to the second being blocked by a barrier). The basic finding was that the subordinates did indeed take into account what the dominants could and could not see. Knowing that the dominants would take all the food they could see, the subordinates went for the food, visible

only to them, more often than they went for the food that both they and the dominant could see. Several control procedures and conditions (one using a transparent barrier that the subordinate apparently understood did not block the dominant's visual access to the food) effectively ruled out simpler explanations in terms of mere behaviour reading.

Second, a study by Call, Hare, Carpenter, and Tomasello (2004) suggests chimpanzees understand something about intentional action. Chimpanzees were presented with a human who had food in his hands and then behaved in different ways, marked as either unwilling or unable to give them the food. There were three conditions in which the experimenter was "unwilling" in different ways, e.g., just staring at the ape, eating the food, teasing the ape with the food. These conditions were each paired with two "unable conditions", e.g., trying to get the food out of a jar, dropping it accidentally, etc. In each group of matched conditions the surface topography of the experimenter's behaviour (body movements and gaze direction) were kept as similar as possible. The main finding was that chimpanzees were more impatient— banged on the cage more, left the area sooner—when the human was "unwilling" than when the human was "unable" (trying but failing), even though they got no food in either case. The chimps in this study behaved as human infants did in a comparison study from 9 months of age (Behne, Carpenter, Call, & Tomasello, 2005).

The upshot of these two studies is that the rudiments of second-order intentionality that develop in human ontogeny at around 1 year are probably not so uniquely human after all; our common cognitive primate heritage runs deeper than previously thought.

COLLECTIVE INTENTIONALITY

Against this background, a broader alternative picture emerges. Basic forms of individual intentionality, both first and second order, develop in human ontogeny in the first one and a half years, but contrary to previous assumptions they develop to some degree in other primate species as well, and so cannot be the sole foundation for uniquely human forms of life. What is uniquely human, however, and a likely foundation of specifically human forms of life is the ability, developing from the second year in human ontogeny, to enter into collective (or "We") intentionality (Tomasello & Rakoczy, 2003; Tomasello et al., 2005).

In collective intentionality two or more subjects share an intentional "we" attitude which is not straightforwardly reducible to individual intentional attitudes.[2] When you and I meet and agree to take a walk together, to use an example from Margaret Gilbert (1990), we form and then pursue the joint We-intention "*We* walk together", which is not reducible to the sum of my individual intention "I walk" plus your analogous one. When I pursue my individual intention to walk and you pursue yours, we might end up walking

beside each other, but not together. When we pursue our We-intention, in contrast, each individual does walk, of course, but acts as part of a joint action (Searle, 2005).

As in the case of individual intentionality, different kinds of collective intentional attitudes can be distinguished: collective beliefs, collective desires, etc. The central cases of collective intentionality for present purposes are arguably the basic ones, namely collective intentions and actions—which constitute the class of cooperative acts and lie at the heart of societal and institutional life.

Clearly, collective intentionality presupposes first-order individual intentionality (for us to walk together I have to be able to walk intentionally myself), and second-order intentionality (for us to walk together I have to track your walking intentionally and adapt to it). But clearly individual intentionality, while being necessary, is not sufficient for collective intentionality. And so the present proposal is that while humans share with other animals simple forms of individual intentionality of first- and second-order, only humans have the ability to build on these to enter into collective we-intentionality.[3]

The relation between individual and collective intentionality is dialectical. On the one hand, human infants are cognitively equipped to understand each other as agents, as potential cooperators, which allows them to enter into collective intentionality and culture. But on the other hand, once children enter into collective intentionality and culture, acquire conventional practices, and above all a language,[4] this in turn shapes and transforms their individual cognitive development by supplying them with new means for thinking, much as Vygotsky and Mead have stressed (Tomasello & Rakoczy, 2003).

Before we turn to the empirical phenomena, some further taxonomic distinctions within the class of collective intentional affairs are relevant (see Figure 5.1, after Searle, 1995). Walking together is an example of a cooperative activity that does not essentially involve the conventional use of objects or any assignment of functions. Though such cooperative activities constitute the most basic form of collective intentionality, their cognitive structure is already quite complex: The individual participants have to understand each other as intentional actors, have to form and pursue a joint intention, and in the course of the joint act they have to be mutually responsive to each others' intentions and acts, often involving division of labour and complementary roles (Bratman, 1992). Crucially, even simple joint activities involve a normative dimension of commitment (Bratman, 1992; Gilbert, 1990).

An important subclass of collective intentionality involves the conventional use of objects and the collective ascription of functions to these objects, e.g., using tools to build something together or using pieces of wood to play chess together.[5] Two kinds of function can be distinguished here with two corresponding degrees of conventionality. *Causal usage functions* are functions we ascribe to objects when we collectively use them instrumentally, i.e., as tools,

Intentional facts

Individual
(I do X)

Individual 2nd order
(I know (you do X))

Collective intentional
= social facts (We do Y)

Collective intentionality
with assignment of functions

Cooperation
(without function assignment)

Causal usage functions
(This is a screwdriver)

Status functions = institutional facts
(This is money)
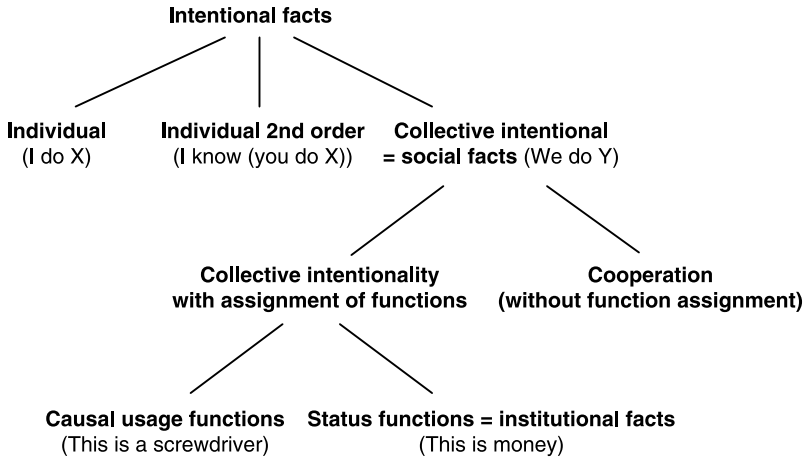
Figure 5.1 Taxonomy of individual and collective intentionality (after Searle, 1995).

and when we design and create objects as tools. The objects fulfil the function partly due to their physical causal make-up, e.g., a knife due to its sharpness. Such causal usage functions are conventional in a weak sense; nothing per se makes a certain object a tool, but we can assign a function to the object simply by making use of its intrinsic physical make-up for our instrumental purposes.

Status functions, in contrast, are conventional in a stronger sense. They are assigned to objects solely as a matter of collective practice; the objects do not fulfil the function due to their intrinsic properties. A slip of paper, for example, is money and a piece of wood is a queen in chess, but one could have decided to pay with wood and play with paper. An object has a certain status function only in virtue of the collective intentional treatment of it as having this status function. Status functions are brought into existence, are constituted by collective intentionality. "X counts as a Y in context C" is the formula that expresses status function creation.

Collective intentionality along with the creation of status functions is what lies at the heart of institutional reality. Status functions create institutional facts, like "This is a queen" or "this is money"; these are observer-dependent facts that only exist in the eyes of the beholders who collectively create them—in contrast to brute facts "out there" like "This is a piece of wood". Institutional reality as a system of status functions pervades our normal adult social life—we live as much in an institutional as in a natural world: We go to work, earn money to pay the rent, own property, are citizens, husbands, or wives, and we utter sounds with semantic status functions (meaning) all day, i.e., speak a language.

Specific normative dimensions are involved in the different forms of collective "We" intentionality. In cooperation, we commit ourselves to pursuing

a joint action and are therefore responsible for trying our best in this pursuit. The assignment of causal usage functions introduces the notions of good functioning and malfunctioning and the notions of appropriate and inappropriate uses of tools. Status functions, finally, involve a specific kind of rule, namely constitutive rules. Whereas regulative rules regulate an already existing activity (e.g., rules regarding on which side to drive regulate driving, which already exists before the rule), constitutive rules bring into existence the very activity they apply to (Rawls, 1955; Searle, 1969, 1995). Formally, "X counts as a Y in context C" specifies a constitutive rule: that X is a Y in the relevant context; and that it is a Y in the relevant context confers normative powers on the objects and carries normative implications (that it ought to be treated as a Y). A piece of wood is a queen in the context of chess and that means it has the power to move in certain ways, ought to be used accordingly, and ought not to be used as firewood in this context, for example.

In sum, collective intentionality involves two or more subjects who share an irreducible "we" attitude, paradigmatically a "we"-intention. Some forms of collective intentionality involve the collective assignment of functions to objects. The strongest form of such functions, status functions, are those that get collectively assigned to objects merely by virtue of convention, when objects are collectively treated as having that function ("counting as something"). Constitutive rules underlie status functions, create institutional reality, and bring with them normative implications—that the objects be treated according to the rules in the relevant context. With this taxonomy in hand, let us now turn to the development of the different forms of collective intentionality in human ontogeny from the second year on, and from a comparative point of view to the question how this development contrasts with that of other species.

Cooperation

Natural observations of human children suggest that during the second year they begin to engage in collaborative games with complementary roles and turn-taking structure and in collaborative instrumental activities with clearly differentiated roles (Brownell & Carriger, 1990; Eckerman & Didow, 1996; Ratner & Bruner, 1978; Ross & Lollis, 1987). In interpreting such observations, however, a fundamental conceptual challenge emerges: how to distinguish instances of cooperation proper from merely socially coordinated behaviour. This challenge is also apparent in interpreting natural observations of complex social behaviours in other animals. Prima facie, social hunting in chimpanzees looks very much like cooperation proper with division of labour (e.g., Boesch & Boesch, 1989). However, on closer inspection many commentators argue that what looks like real cooperation turns out merely to be complicated social coordination in which each participant plans and acts individually, while the impression of collectivity emerges from the contingency between the individual's behaviours due to external constraints (one individual starts

hunting at a certain place, then the next individual starts hunting, but cannot take the same place, then the third individual has to take even another place, etc.; Tomasello & Call, 1997; Tomasello et al., 2005).

To illustrate the challenge, consider Gilbert's (1990) walking example. Imagine two people taking a walk together. And now imagine two people that happen to walk beside each other at the same pace on a pavement, e.g., heading towards the same bus station. Both cases might look virtually the same (in both cases the two participants walk at the same pace, coordinate in the sense of looking where the other is currently walking, and wait when only one can get by, etc.). What we would usually do to find out whether this is a joint walk or just a coincidental parallel walk is to ask the participants what they are doing and consider their answers, e.g., "We're taking a walk" or "I'm walking to the station". So, the challenge is to distinguish the two cases in prelinguistic children or nonlinguistic animals.

Fortunately, the two cases may look very much alike, but not identical. In particular, different courses of action are to be expected in the case of obstacles to the pursuit of the joint goal.[6] When partner A cannot keep up with the pace of B, for example, B is committed to adapting her pace, and will usually do so (Gilbert, 1990). Or if she doesn't, then A will usually not only be surprised but offended ("But didn't we want to walk together?"). Similarly, if B stops walking for no obvious reason, A will usually reengage her ("Hey, come on!"). These responses are not to be expected in the case of mere coordination (the just coincidental parallel walking), because they are indicative of the specific commitment inherent in joint actions.

Recent experimental studies have employed these specific differences to test for young children's and chimpanzee's ability to engage in cooperation proper. Warneken, Chen, and Tomasello (2006) directly compared children (18 and 24 months old) and human-raised chimpanzees on experimental tasks that required collaboration with an experimenter. Some of these tasks had an instrumental problem-solving structure (toys for the children/food for the chimps could be obtained through an apparatus that had to be operated together), others were ends-in-themselves, collaborative games. During the collaborative acts, the experimenter was programmed to interrupt the shared activity at a predetermined point (by ceasing to perform his role) to see if the subjects would attempt to reengage his participation.

Children engaged proficiently in both kinds of collaborative tasks and during the interruption periods they communicated appropriately with the experimenter, e.g., pointed to his side of the apparatus, and tried to reengage him in the collaborative activity. Chimpanzees, in contrast, engaged with the experimenter in a coordinated way only in the instrumental tasks where a food reward was to be gained, but not in the noninstrumental game acts. Furthermore, even in the instrumental tasks, when the partner interrupted his engagement, they never communicated with him or tried to reengage him in the collaborative activity, rather they tried on their own or disengaged.

Another crucial difference between cooperation proper and mere social

coordination is that the former often involves division of labour, the assignment of complementary roles to different participants. With regard to the grasp of such role structures of joint activities, Carpenter, Tomasello, and Striano (2005) tested 18-month-old children in the context of novel collaborative games with an experimenter. First the experimenter played one role and the child learned to play the complementary one. In a second phase the children then spontaneously performed role-reversal imitation, i.e., acted out the other role when appropriate and thus indicated an awareness of the complementary role structure of the game. Three human-raised chimpanzees, in contrast, though they had acquired some imitative abilities through enculturation, revealed little competence for such role-reversal imitation (Tomasello & Carpenter, 2005).

Taken together these studies suggest that during the second year of human ontogeny children develop a nascent ability to engage in cooperative activities as the basic form of collective intentionality. On a simple level, they form and pursue shared "we" intentions with others, with a rudimentary awareness of the commitments and role structures characteristic of cooperative enterprises. The behaviour of chimpanzees, in contrast, does not necessarily warrant the ascription of collective intentionality proper, but might plausibly be characterized as complex social coordination only.

Collective function assignment and the foundations of institutional reality

Objects such as tables, nut-crackers, carburettors, or pens have causal usage functions and they have them essentially in virtue of the collective assignment of these functions to them. A stone might be very useful for cracking nuts, might afford nut cracking. But a regular stone is not "for" cracking nuts, and is not "broken" when it fails to crack nuts—in contrast to established nut-crackers (which might be stones).

Infants in their first year and many other animals do use tools individually. But does this imply they have any grasp of the collective assignment of usage functions to objects? Probably not. What has to be distinguished is using and understanding tools in a wide instrumental sense ("this stone affords nut-cracking") and understanding function assignment in a more narrow, normative-teleological sense ("this is a nut-cracker, that's how we use it and that's what it's *for*. If it doesn't crack, it's broken").

These two forms of understanding can easily be distinguished in older children with verbal interview methodology. And preschool children reveal rich knowledge about teleological ascription of functions to artifacts when talking about them (e.g., German & Johnson, 2002; Kelemen, 1999). But how do we know about younger children? One source of evidence comes from naturalistic observations: Children in their second year begin to use teleological normative vocabulary in describing malfunctioning artifacts as "broken" (for example, Kagan, 1981). Another source of evidence comes from imitation combined

with so-called "functional fixedness" (Duncker, 1945), the phenomenon that we find it hard to use artifacts in ways that deviate from their normal use. Imitation of conventional acts with artifacts alone from around age 1 might already be viewed as an index of understanding artifact functions. But imitation alone clearly cannot distinguish such a rich understanding from a simpler, affordance-based one. More plausibly, functional fixedness, however, can be interpreted as an index of understanding the conventional usage of artifacts, of the ways "we use them". Recent experimental studies have revealed that children from 2 years show just this kind of fixedness after imitating novel acts with artifacts (Casler & Kelemen, 2005). They are reluctant to use an artifact for purposes other than the one it was introduced for or to use a different artifact for a given purpose in place of the one introduced for it. Nonhuman primates, in contrast, seem not to be good imitators at all, and we have no evidence for imitative learning involving functional fixedness in any other species. Thus, while many animal species use tools in complex ways, only human children seem to develop an appreciation of the creation of artifacts as objects with collectively assigned usage functions.

Let us now turn to collective intentionality with the assignment of status functions. This form of collective intentionality, as we saw above, lies at the heart of institutional reality without which human society would be virtually inconceivable. And it is here that the dividing line between human sociality and that of other species can be seen most clearly (Searle, 2005).

Money and political leadership are obvious examples of status functions, but from an ontogenetic point of view, it is equally obvious that young children early in development do not have much of a grasp of such phenomena. I would like to suggest that playing games serves as a potential cradle for children's entry into collective intentionality with status function creation (see Rakoczy, 2006, 2007; Rakoczy & Tomasello, 2007). In fact, adult rule games such as chess are among the paradigmatic examples for practices involving status functions, e.g., "This piece of wood counts as a king in the context of chess". Of course, 2-year-olds don't play chess, but from the second year children do begin to engage with others in playing simple rule games, and in particular, games of pretence.

Take the example of some great pretenders, the toddler twins Adam and Eve. Eve takes a tennis ball, puts it to her nose and says "Hm, how delicious this apple is". She then offers it to Adam ("Here, have some"), who starts to make peeling movements on the ball with a toy knife. He then puts the ball to his mouth and makes enthusiastic chewing movements and "Yum" sounds. Eve joins in and finally they close the episode by saying "All gone, eaten up". Though this is not an instance of playing an established game with fixed rules, it is an instance of collectively playing a game with the assignment of transient status functions, making up ad hoc constitutive rules on the spot. "This ball *counts as* an 'apple' in our pretence context" is the central status function assignment and others follow—"It counts as peeled now" and then "It counts as eaten up now".

These assignments bring with them a normative structure of the joint activity. Some pretence acts are inferentially licensed in the game, others are not. Pretending to peel the ball/apple, pretending to eat it or to bake a cake with it are licensed, pretending to drive it or pretending to fax it are not (Walton, 1990).

From a comparative point of view, pretend play is quite clearly a uniquely human phenomenon. Although there are anecdotes of pretence-like behaviour in some human-raised animals (reviewed in Mitchell, 2002), these are difficult to interpret and generally it is quite clear that no other species reliably engages in pretend play as we know it (for reviews of precursors to pretend play in great apes, see Gómez & Martin-Andrade, 2002, 2005). Ontogenetically, children usually start to engage in simple pretend play in their second year. Early pretence is probably acquired by imitation (El'Konin, 1966; Rakoczy, Tomasello, & Striano, 2005), usually first occurs with caregivers (Haight & Miller, 1992; Slade, 1987), and centres around replica objects (e.g., toy cups and plates) and simple corresponding pretence actions (e.g., pretending to eat and drink) (e.g., Elder & Pederson, 1978).

But when they begin to engage in joint pretending, what do young children understand about the logical structure of pretence? In particular, to what extent do they grasp the normative and inferential structure created in shared pretence scenarios? In an elegant set of studies, Harris and Kavanaugh (1993) showed that children from 2 years do seem to grasp the normative structure created through joint pretence stipulations and engage in inferentially appropriate pretence acts. When the experimenter pretended to pour tea into a cup, for example, children pretended to drink from the cup. When the experimenter pretended to spill tea on the table, children pretended to clean the table.

Based on these studies, we recently tested young children in even more stringently designed situations (Rakoczy & Tomasello, 2006; Rakoczy, Tomasello, & Striano, 2004). Children (old 1-year-olds, young 2-, and young 3-year-olds) saw pairs of superficially analogous incomplete as-if-behaviours with objects: pretending to do an action and unsuccessfully trying to do the same action, e.g., pouring from a container into a cup. In both cases the actor would make pouring movements with a novel container over a cup, but without actual pouring happening. In one case, he would mark it with signs of playfulness and sound effects as if pretending to pour, in the other he would mark it with signs of surprise and frustration as if really trying to pour. Importantly, the container really did contain water and thus could really be used to pour. The logic is the following: In both cases the child sees superficially analogous movements, but they constitute radically different intentional actions. In the trying case the model wants to properly perform the action but fails. If the child understands the intentional structure of the model's act, this licenses the inference "If I want to do the same, other means should be used". In the pretence case, in contrast, the model performs an intentional pretence act involving the assignment of a status function ("This act counts as pouring"

and "The cup counts as full now"). If the child understands this as such, it licenses the child's entering into a joint we-pretence organized around this status function ("We pretend that the cup is full now") with appropriate inferential pretence acts, e.g., pretend to drink from the cup that the model had pretended to pour into.

Two- and 3-year-olds (and to some lesser degree old 1-year-olds) showed this systematic and differential response pattern: After "trying" models, they themselves really performed the action or tried to, but by different means, e.g., using a tool to open the container first and then pouring. After "pretence" models, in contrast, they performed appropriate inferential pretence acts, e.g., pretended to drink from the cup into which the model had pretended to pour. This systematic pattern of responses is best interpreted, I suggest, as follows: In both cases children discern the intentional structure of the model's behaviour and respond accordingly. In the trying case, children perform an appropriate individual instrumental act. In the pretence case, however, they join into a collective we-pretence centred round the status function introduced by the model's overture.

That is, young children respect the inferential structure that comes along with collective intentionality and status function assignment, as indicated in their own actions. But what do they understand about the normativity that status functions introduce? Are they really following a rule or are they just acting in accordance with a rule? Do they indicate an awareness of the normative structure more directly and explicitly than in their own acts? Would they not only act correctly themselves, but criticize others for incorrect acts? This is crucial as critique, beyond mere surprise, in response to incorrect acts is the hallmark of appreciating normative structure; mere surprise is the appropriate response when there are acts deviant from purely statistical regularities.

In a recent study I addressed this issue (Rakoczy, in press). Two- and 3-year-olds were engaged in games of pretence with status functions assignment to objects. For example, with a pile of clothespegs, one clothespeg was pretended to be a knife, all others were pretended to be carrots. The child and the adult pretended to peel the carrots with the knife and cook and eat the carrots. Then at some point a third character (a puppet) came, joined into the pretence ("Oh, may I join your game?"), and in the target condition performed pretence acts that were normatively inappropriate in the light of the status functions of the objects, e.g., she pretended to eat the clothespeg that was the knife. In the control condition, the puppet pretended appropriately. Three-year-olds (and to a lesser degree 2-year-olds) frequently protested explicitly against such violations of the constitutive rules of the pretence game, e.g., "No, that's not a carrot, that's our knife!" in the experimental condition, but were content in the control condition.

In sum, in joint games of make-believe young children from 2 actively and knowingly participate in collective intentionality with status function creation—as indicated both in their own competent inferential actions and in their normative responses to other's mistakes.

Similar patterns were also found regarding young children's playing of simple rule games. In a recent set of studies (Rakoczy, Warneken, & Tomasello, 2008) we applied a logic similar to that in the pretence study mentioned earlier. Children of 2 and 3 years of age were engaged in a joint game with a partner, when at some point a third character, a puppet, came, wanted to join the game, but violated the constitutive game rules. Again, in all three studies the children protested in response to the puppet's mistakes frequently (but hardly did so in a control condition where the very same behaviour was performed, but the context was changed such that it was now not a mistake). That is, the 2- and 3-year-olds understood the normative structure of the game rules, i.e., the constitutive rules, also appreciating the context relativity of this normative structure.

In embryonic and isolated form we thus have here the basic structure of institutional reality in the games of 2- and 3-year-olds. Of course this is a long way from money, marriage, and universities, but the seeds are there, and so joint pretending and playing other games quite plausibly can be considered the central cradle for and the entrance gate to institutional life.[7]

SUMMARY AND CONCLUSION

Humans live complex social lives and so do countless other species. Humans, though, are not only social beings, as are other animals, but participate in cooperative, societal, and institutional ways of life that are quite clearly unique on this planet. Traditionally, individual intentionality was supposed to be the monopoly of humans that explained why only humans talk and have culture. But today in light of the impressive parallels discovered in the early development of individual intentionality in humans and in other species, there is little plausibility to such a story. For a while second-order individual intentionality ("theory of mind") seemed a likely successor candidate for explaining uniquely human sociality. And while complex second-order intentionality, i.e., ascribing epistemic attitudes to each other etc., is surely a uniquely human achievement and an important foundation for many uniquely human ways of life (self-consciousness, full-fledged communication, etc.), recent research with apes suggests that at least simple forms of second-order intentionality aren't as uniquely human as once thought.

What thus emerges as the likely core of the uniquely human cognition which underlies uniquely human sociality is the ability to enter into irreducibly collective "we" intentionality. Different forms of this ability develop from the second year on: the ability to engage in shared "we" activities with others, opening up the space of cooperation, and the ability to participate in collective practices with the assignment of functions, in particular status functions, opening up the space of institutional reality.

The human animal is essentially a collective animal, and ontogenetically it becomes so from very early, from the second year of life. This presumably

is the point where humans begin to leave all other animals behind and grow into a community of sharing "we" intentions and practices, an essentially normatively structured public space that is constitutive of full-fledged personhood.

ACKNOWLEDGEMENT

NOTES

1 I am speaking of "simple" intentionality here, as arguably many forms of full-fledged human individual intentionality are essentially dependent on language, a point I will return to later (see Bermudez, 2003, for a proposed taxonomy of simple nonlinguistic intentionality in contrast to linguistically mediated intentionality).

2 For the central works in recent analytical philosophy on this, see Bratman (1992), Gilbert (1990), Searle (1990, 1995, 2005), Tuomela (1995), and Tuomela & Miller (1988). For an overview, see Tollefsen (2004).

3 In other words, the "Machiavellian Intelligence Hypothesis" (Byrne & Whiten, 1988) with its emphasis on the social cognition underlying individual manipulation of conspecifics (i.e., a form of individual second-order intentionality) might well be adequate for nonhuman primates, but falls short of adequately describing the inherently collective dimension of human social cognition.

4 I will here hardly touch upon the development of language and its relation to collective intentionality—as this would easily go beyond the scope of the present chapter. On the one hand, language as a conventional practice is itself an instance of collective intentionality and thus in some sense secondary to collective intentionality. On the other hand, language is in some sense the fundamental collective activity without which many other collective practices would not be conceivable.

5 Strictly speaking, functions are not only assigned to objects, but to actions as well (and, in fact, actions are logically the primary case—the status of objects is dependent on relevant actions one can do with the objects). Language is the paradigmatic example: Emitting such and such sounds in the right context according to the right rules counts as speaking. But I will here focus on the case of object functions, first because regarding objects the general forms of collective intentionality can best be illustrated. And second, because ontogenetically it is plausible that children come to understand function assignment to objects before they understand it in the case of actions.

6 In analogy to the case of individual intentional acts: Persistence in the presence of obstacles is usually a good criterion to distinguish goal-directed action proper from just seemingly goal-directed behaviour.

7 Of course, language is the first instance of collective intentionality involving status functions into which young children enter in rudimentary form from 1 year on. However, and this is one of the reasons why I haven't touched upon language in this context, arguably young language learners do not have to have any understanding whatsoever of the logical status of constitutive rules and the creation of status functions. Children up to the age of at least 4 or 5 just do not view language sounds as phonologically or syntactically defined events or objects (brute facts) that

additionally are assigned meaning (institutional facts). They hear through the sounds, directly perceiving them as meaningful (as we all normally do when we do not take any kind of metalinguistic stance). The situation is different in the case of games, however, because there status functions are assigned to physical objects that children surely see as such. This is especially clear in the case of pretence (e.g., "this tennis ball counts as the apple in our pretence") where children have to at least implicitly distinguish the brute fact about the object (it's a ball) from its status function ("apple") in the game.

6 Socio-cognitive abilities and cooperative breeding

Judith-Maria Burkart

HOW CAN WE LEARN ABOUT EXCLUSIVELY HUMAN TRAITS FROM ANIMALS?

Prima facie, studying animals in order to learn about uniquely human traits does not seem very promising. If certain traits are really unique to our own species, they must be investigated in humans where they actually occur. While this is the only way to obtain a detailed characterization of uniquely human features, there are important questions that this approach cannot answer. First, it cannot provide fundamental information on whether a given feature actually is unique to our own species or not. In principle, one would have to test all living species before drawing such a conclusion. In practice, however, we must rest content with excluding the presence of potentially unique human features in as many species as possible—at least in those species where they are most likely to occur, i.e., in apes and to a lesser extent in monkeys. But even once a feature can confidently be labelled as one that does not occur outside the human context, detailed knowledge of its architecture, functioning, or ontogeny during childhood, derived from studies of our own species, still offers only a limited view of that feature. A comprehensive understanding also has to encompass knowledge of its evolutionary origins, e.g., information on whether we can determine evolutionary precursors, what they look like, and how they are distributed among nonhuman animals. This will inform us about which transitions took place over evolutionary time and perhaps why.

The comparative approach

Besides identifying those abilities that actually are unique to humans, the most straightforward way in which studying animals can contribute to an understanding of our own traits is the traditional comparative approach (e.g., Byrne, 1995; Lorenz, 1950). The comparative approach allows us to characterize hypothetical common ancestors. This can be achieved by inferring that the features that are present in all extant species descended from this ancestor were most likely present in that ancestor. By comparing hypothetical

ancestors that are differentially distantly related in chronological order down to the last common ancestor that we shared with chimpanzees and bonobos, we can trace the likely evolutionary course of the emergence of cognitive abilities that in their most complex form may only be present in humans.

An inherent limitation of the traditional comparative approach is that it cannot inform us about what happened during the last 5–7 million years of hominization, after our lineage split from those of other great apes (Fischer, Pollack, Thalmann, Nickel, & Pääbo, 2006; Hacia, 2001). Even though this lineage continued to subdivide into many branches, the only surviving species is our own. While the fossil record allows us to extrapolate the evolution of morphological traits during this period, the situation with regard to behavioural or cognitive traits is far less promising. Although some archaeological artifacts such as tools, evidence for the use of fire, sophisticated burial sites, or artistic relics permit inferences concerning a minimal set of cognitive requirements (Mithen, 2001; Parker & McKinney, 1999), the available evidence remains scarce and hard to interpret, especially for the earlier forms that were less like modern humans.

An alternative way to learn from animals

The traditional comparative approach is not the only way in which we can learn from animals. If we compare morphological features, behaviours, or cognitive abilities across many different species, we often observe clusters of traits that emerge in some species, but not in others. What characterizes such species is not necessarily their close phylogenetic relationship but rather that they shared important environmental conditions over evolutionary time and convergently evolved similar adaptations in response to them. For example, the reduction of body surface in order to minimize loss of energy is a common adaptation to rough climatic conditions and can be observed in a variety of species (Meiri & Dayan, 2003), all showing more compact body shapes in colder environments than their sister species in warmer environments. This compact body shape is not a consequence of common ancestry but a convergent solution to the same problem. Similarly, primates living in despotic rather than tolerant societies show highly formalized signals of submission, whereas those in less despotic societies only show formal dominance signals and those in very egalitarian ones do not show any formalized signals at all (Preuschoft & van Schaik, 2000). Hence, both ecological and socioenvironmental constellations can exert specific adaptive pressures that result in consistent patterns of consequences, thereby promoting convergent adaptations.

Thus, an alternative to the traditional comparative approach lies in attempting to identify the ecological and social constellations that had major impacts during our phylogenetic past, preferentially during the last five to seven million years. If some of these environmental constellations consistently produce highly similar adaptations in diverse species, we can also expect corresponding consequences or response patterns in the context of hominization. Hence,

if we find such a response pattern in humans but not in our closest living relatives and can show at the same time that corresponding environmental challenges were faced by our species in evolutionary time, we do not have to construe the response pattern as a uniquely human trait. Rather, it can be considered a direct response to this specific social or ecological challenge that could be expected to arise in any species exposed to it.

One such environmental constellation is cooperative breeding, a reproductive system in which individuals other than the genetic parents help rear their offspring. This breeding system presumably provided a crucial context for human development and links to our unique cognitive abilities have been discussed (Chisholm, 2003; Hrdy, 1999, 2005b). In this chapter I will pursue the alternative approach to learning from animals, outlined previously, by analysing the cognitive consequences that the cooperative breeding system can have on nonhuman primates. Specifically, I will focus on the cognitive performance and abilities of the cooperatively breeding callithrichid monkeys. By characterizing possible functional pathways that might link cooperative breeding systems to cognitive functioning, I will try to identify the role that cooperative breeding might have played during hominization.

COOPERATIVE BREEDING AND ITS CONSEQUENCES IN NONHUMAN PRIMATES

Correlates of cooperative breeding: Life history traits and behavioural propensities

Broadly defined, cooperative breeding is a reproductive system in which group members other than the genetic parents (alloparents) help one or both parents rear their offspring (Hrdy, 2005b, p. 10). In mammals cooperative breeding is reliably associated with a number of life history traits as well as behavioural propensities. A direct consequence of such a reproductive system is that female breeders can produce more offspring because the costs of reproduction per single offspring are shared among different group members. These saved energetic resources can be invested in producing more offspring, by increasing litter size, decreasing interbirth intervals, or by producing bigger infants. Moreover, for the mother, the independence of previous offspring is no longer a limiting factor for producing the next (set of) offspring, because other group members can take over the care of older infants when she is occupied with the newborns. Hence, the cooperative breeding system allows the unusual coexistence of short interbirth intervals and slow maturation of immatures (Hrdy, 2005a; Langen, 2000). Cooperative breeding also has consequences at the behavioural level. With group members interested in the survival of the same immatures, within-group competition is reduced. This mutual interdependence results in highly tolerant social relationships and low levels of aggression among group members (Digby, 1994; Schaffner &

Caine, 2000; Sutcliffe & Poole, 1984). Finally, once a cooperative breeding system is firmly established in a species, the reproductive success of mothers depends on the degree of allomaternal assistance that is available. As a consequence, mothers in such species are sensitive to both quantity and quality of helpers and, in extreme cases, abandon their offspring if no sufficient allomaternal care is perceived (Hrdy, 1999).

Among nonhuman primates, cooperative breeding systems are found in all callithrichid monkeys, a family of small neotropical primates, consisting of tamarins and marmosets (Rowe, 1996). They typically live in family groups composed of a breeding pair and its adult offspring. Instead of leaving the group and becoming reproductively active themselves, these adult offspring stay with their parents and help raise their younger siblings. Except for breastfeeding, the main caregivers are often the father and older siblings; they carry the infants most of the time and share food with them (Brown, Almond, & van Bergen, 2004), and also cooperate in group defence and share vigilance duties (Bales, Dietz, Baker, Miller, & Tardif, 2000). As a consequence, young marmosets, when in distress, preferentially run to the one who carried them the most, usually their father or oldest brother, and not their mothers (Kostan & Snowdon, 2002).

Social bonds between group members are very strong and not seriously threatened even if aggressive conflicts arise. After such incidents, the animals that were involved do not reconcile consistently, but usually quickly resume their previous behaviours. Reconciliation functions to restore damaged relationships; it has been documented in over 30 primate species. The lack of consistent reconciliation indicates that conflicts in cooperatively breeding primates hardly ever damage their stable relationships (Aureli & Schaffner, 2006).

Cognitive correlates of cooperative breeding in nonhuman primates

Besides having life history and behavioural consequences, cooperative breeding may also be associated with enhanced cognitive functioning. According to the Cooperative Breeding Hypothesis developed by Sarah Hrdy (1999, 2005b), cooperative breeding was a crucial context during human evolution that shaped many of our uniquely human features. This hypothesis has the potential to explain not only many of the otherwise puzzling peculiarities of the human reproductive system and development, but also why our ancestors, unlike those of great apes, managed to move into and spread across new habitats without losing immatures, who are most susceptible to starvation. In addition, this hypothesis also suggests that our uniquely complex cognitive abilities, especially in the social context, are linked to the cooperative breeding system (Chisholm, 2003). A link between cooperative breeding and enhanced cognition and communication seems to be present in callithrichids as well (Snowdon, 2001b), giving rise to the question how cooperative breeding could enhance cognitive functioning.

Cognitive performance of callithrichids

On the assumption that cooperative breeding has an impact on cognitive performance, we would expect callithrichids to behave more skilfully than other monkeys in different contexts. Indeed, accumulating evidence both from naturalistic observations and experimental studies suggests that callithrichids perform particularly well in the context of communication, social learning, simple forms of teaching, and cooperative problem solving. Snowdon (2001b) reviewed literature on communicative and cognitive performance in callithrichids and found various peculiarities, e.g., that they tend to show higher vocal plasticity than other monkeys. For instance, they modify both call structure and usage in different social and environmental contexts and with changes in social status, and infants pass through a babbling phase during ontogeny.

Social learning is another domain in which callithrichids might outperform other monkeys. For example, tamarins can learn to avoid noxious foods through observation, contrasting with results from other monkeys in comparable experimental situations (Snowdon & Boe, 2003). Observational forms of social learning such as imitation are very rare in nonhuman primates and their presence has been questioned for years even in great apes (Dautenhahn & Nehaniv, 2002). Although many taxonomies and definitions of the various forms of social learning exist (Call & Carpenter, 2002; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004), there is a consensus that observational forms of social learning are the most complex and can be classified according to which aspects of the behaviours are copied, e.g., goal, result, or the topography of the action. Copying of the exact topography of an action has been found in great apes (Horner & Whiten, 2005; Whiten et al., 2004); the only monkey species in which such imitational learning could be demonstrated are cooperatively breeding common marmosets (Bugnyar & Huber, 1997; Voelkl & Huber, 2000; but see Caldwell & Whiten, 2004).

The efficiency of social learning can be increased if the demonstrator engages in teaching behaviour, i.e., if she modifies her behaviour in the presence of a naïve observer, thereby encouraging or punishing the observer's behaviour or providing experience, which results in a learning benefit for the observer and is costly to the teacher (Caro & Hauser, 1992). The prevalence of teaching in the animal kingdom is even lower than that of imitation learning (Csibra, 2007; Leadbeater, Raine, & Chittka, 2006) and, even in apes, potential instances are rare. Rather than actively teaching their young, typical social learning situations in apes consist of mothers displaying increased levels of tolerance towards their curious, eagerly learning offspring (King, 1994, 1999). Foraging is the most common context for social learning and potential instances of teaching to occur. However, in apes even mother–infant food sharing events are solicited by the begging infant rather than initialized by the mother (Goodall, 1986; Maestripieri, Megna, & Ross, 2002; Nishida & Turner, 1996; Ueno & Matsuzawa, 2004).

In contrast, food sharing events in callithrichids can also be initialized by the caregiver who holds a food item in an outstretched hand and emits a vocalization that results in an infant approaching and taking it (Bales et al., 2000; Brown et al., 2004; Feistner & Price, 1990, 1991, 2000; Ferrari, 1987). The active role of caregivers in food-sharing events, together with the fact that food transfers peak around weaning and are most likely to involve novel or difficult-to-process items, raise the possibility that this behaviour is an instance of teaching. Infants indeed benefit from food transfers by starting to feed independently earlier, but also by learning in which contexts food-related vocalizations are appropriate (Roush & Snowdon, 2001). Furthermore, Rapaport and Ruiz-Miranda (2002) reported observations from wild golden lion tamarins where adults directed immature offspring to locations where hidden prey items were located without retrieving them themselves, again indicating an active role of adults for the acquisition of skills by immatures.

Finally, recent evidence also suggests that callithrichids might be more likely than other primates to solve cooperation tasks. Common marmoset dyads successfully coordinate their behaviours both locally and temporally, without dominants monopolizing the apparatus and reward or forcing subordinates to cooperate (Werdenich & Huber, 2002). Furthermore, experiments with cotton-top tamarins suggest that they even understand the roles of their partners in cooperation tasks, a cognitive ability thought to be present only in great apes (Cronin, Kurian, & Snowdon, 2005).

However, there are also domains where callithrichids are far less proficient, not only in comparison to the domains discussed earlier, but also in comparison to other monkeys. Tool use in the wild, for example, is indeed very rare and as far as known, restricted to great apes and capuchin monkeys (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Goodall, 1986; Moura & Lee, 2004; van Schaik, 2004). However, in captivity spontaneous tool use is reported from many primate species, but not from callithrichids (van Schaik, Deaner, & Merrill, 1999); they also have lower innovation rates compared to most other primates, and the same is true for performance in learning set tasks (Lefebvre, Reader, & Sol, 2004). Finally, in a meta-analysis of a large number of cognition studies from nine different experimental paradigms in strictly nonsocial contexts, Deaner, van Schaik, and Johnson (2006) found again that marmosets were systematically outperformed by most other primates. Therefore, the current picture suggests that although we find evidence for enhanced cognitive performance in the social context, the same is not true in nonsocial domains.

Superior performance or superior ability?

The apparent dissociation between social and nonsocial cognitive performance in marmosets and tamarins raises the question as to what extent related cognitive abilities underlie this unexpected performance. All the tasks in

which callithrichids seem to outperform other monkeys are from the socio-cognitive context. To solve such tasks, humans rely heavily on their Theory of Mind, i.e., the understanding that other individuals possess mental states such as perceptions, desires, knowledge or beliefs and that these mental states are responsible for generating behaviours (Heyes, 1998). Whether any non-human primate has a Theory of Mind has been hotly debated since Premack and Woodruff (1978) first raised the question. Ontogenetically, human children acquire a full-fledged Theory of Mind by 4 years of age, when they understand that others can have beliefs that do not coincide with the real status of the world, as demonstrated by passing false belief tasks (Wimmer & Perner, 1983). Using the understanding of false beliefs as criterion, nonhuman primates clearly do not have a Theory of Mind (Call & Tomasello, 1999).

However, long before human children understand beliefs, they grasp other mental states such as desires and perceptions (Baron-Cohen, Tager-Flusberg, & Cohen, 2000; Perner, Sprung, Zauner, & Haider, 2003; Wellman & Wooley, 1990). Without denying the importance of passing false belief tasks, conceptualizing Theory of Mind in terms of the developmental trajectories involved in understanding different psychological states provides a more fruitful strategy, compared to viewing Theory of Mind as an all-or-nothing phenomenon (Malle, Moses, & Baldwin, 2002).

The performance of callithrichids in sociocognitive tasks raises the question whether they are able to solve such tasks by using a Theory of Mind. Given that the all-or-nothing perspective is being abandoned both in developmental and comparative psychology and that visual perceptions are among the easiest mental states to grasp, for both children and apes, a fair question to ask is whether common marmosets possess this component of Theory of Mind and understand visual perspective. To test this we used a setting that had originally been used to demonstrate the understanding of visual perspective in chimpanzees (Hare et al., 2000) and in which a subordinate and a dominant individual are facing each other in the outer compartments of an experimental room (Figure 6.1a; Burkart & Heschl, 2007).

Two pieces of food were placed in the middle compartment, separating the animals from each other. One piece of food, sitting on top of a T-shaped bar leading from one side of the middle compartment to the other, was freely visible to both animals, but the second one was only visible to the subordinate because it was positioned on the subordinate's side of this T-shaped bar. If the subordinate animal understood that the second piece of food was not visible to the dominant partner, it was predicted to take the piece of food that it alone could see. Subordinate marmosets behaved precisely this way and consistently chose the piece of food that was only visible to them (Figure 6.1b). The fact that the T-shaped bar ran across the experimental room from one side to the other excludes the possibility that the subordinates' choice behaviour was due to a preference to eat near such a bar. In addition, subordinates were given a small headstart that forced them to make their own choice, instead of simply reacting to the choice of the domi-

(a)

(b)
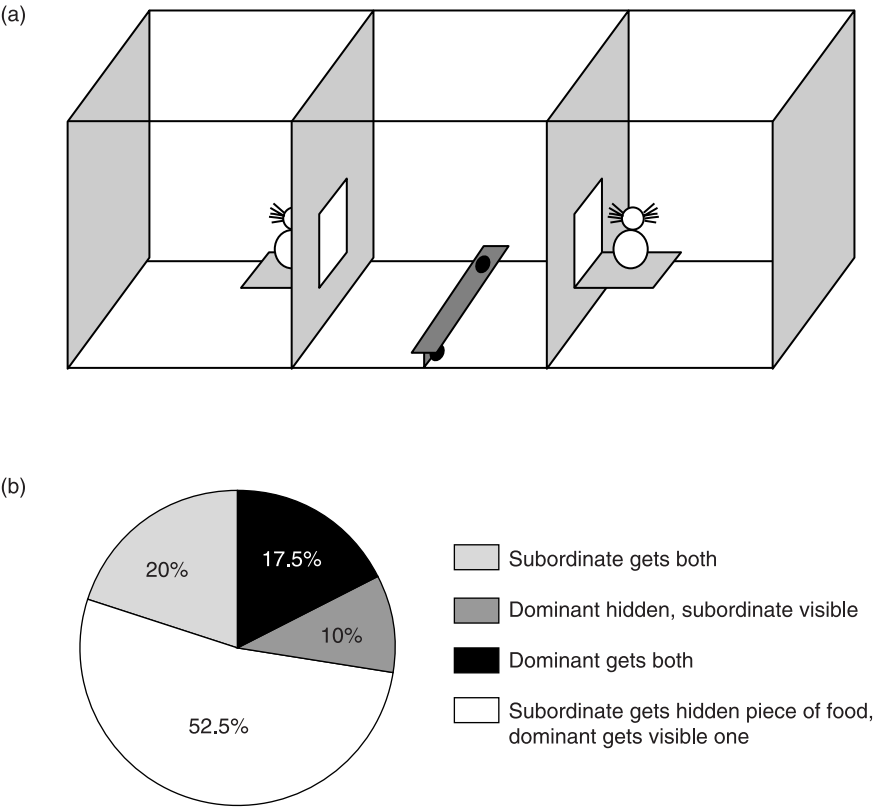
Figure 6.1 (a) Experimental setting for testing common marmosets' understanding of visual perspective (after Hare et al., 2001). While the dominant marmoset in the left compartment sees only one piece of food because the second one is hidden from its view, the subordinate marmoset in the right compartment can see both pieces. If the subordinate understands that the dominant from his position can only see the freely visible piece of food, it would choose the hidden one. (b) The outcome of encounters where subordinate marmosets saw both pieces of food and got a small headstart indicates that they understand visual perspective.

nant individual who, of course, would head for the piece of food that was visible to her. Furthermore, when the roles were reversed during a control condition and the dominant saw both pieces of food and got a headstart while the subordinate only saw one piece of food, dominants did not preferentially retrieve the hidden piece of food, further indicating the flexibility of the choice behaviour to the social context. Finally, almost all subjects, with the exception of the lowest and the highest ranking, participated both as dominant and subordinate in the test, according to their dominance status within a given dyad. The flexible adaptation of their behaviour in the test, according to their changing dominance status in different test dyads, confirms their understanding of the situation.

The behaviour of the marmosets in this experiment suggests that they

understand visual perspective, i.e., what others can or cannot see (Level 1 perspective taking; Flavell, 1985). The marmosets therefore behaved like chimpanzees, which exhibited the same choice behaviour, but unlike capuchin monkeys that were tested with the same experimental paradigm (Hare et al., 2003). Thus, the results lead to the conclusion that common marmosets, like chimpanzees but unlike capuchin monkeys, possess this simple Theory of Mind ability. Given the far-reaching implications of such a conclusion, we opted to confirm our findings and assessed visual perspective taking in a second set of studies using a different experimental approach.

To validate the previous findings we built on earlier results demonstrating that marmosets are able to use cues given by an experimenter in order to locate hidden food (Burkart & Heschl, 2006). The ability to use experimenter-given cues is usually tested with the object choice paradigm in which a subject has the choice between two containers, one baited with a piece of food, while a human experimenter cues the baited container, e.g., with tap, point, or gaze cues. Passing object choice tasks is notoriously difficult for nonhuman primates (Anderson, Montant, & Schmitt, 1996; Anderson, Sallaberry, & Barbier, 1995; Call, Agnetta, & Tomasello, 2000; Vick & Anderson, 2003). In earlier experiments we showed that marmosets can solve this task if the probability of success by chance is lowered by offering the choice between more than two containers, in our case nine or six containers. This result also indicates that they extrapolate gaze direction accurately to a specific target object, rather than coorienting in a reflex-like manner with the experimenter and subsequently taking the first container they happen to see.

We used the same sample of marmosets that previously had been demonstrated to use a range of experimenter-given cues, including eye-only cues, under the conditions described previously in the object choice paradigm. In order to test their understanding of visual access, we introduced a number of modifications to the test setting (Figure 6.2a). The animals again had a choice between six containers. However, they were no longer arranged in full view of the experimenter, but attached to two sides of a wooden board so that each container on one side of the board had a counterpart in exactly the same position on the other side. Facing the edge of the board, the marmoset from its starting position could see all six containers as well as the human experimenter cueing the baited container from one side of the board. In order to localize the bait now, it was no longer sufficient to correctly extrapolate gaze direction because it would always indicate two containers, the correct one and its counterpart on the other side of the board. In addition, the marmoset also had to understand that the gaze of the human experimenter cannot penetrate a solid object, i.e., what the experimenter actually could or could not see. Surprisingly, the marmosets no longer showed an understanding of visual access. While they still extrapolated the gaze direction correctly and tended to choose one of the two containers in the experimenter's line of sight, they were unable to discriminate which side of the board the gaze led to (Figure 6.2b).

Thus, while common marmosets were able take into account the other
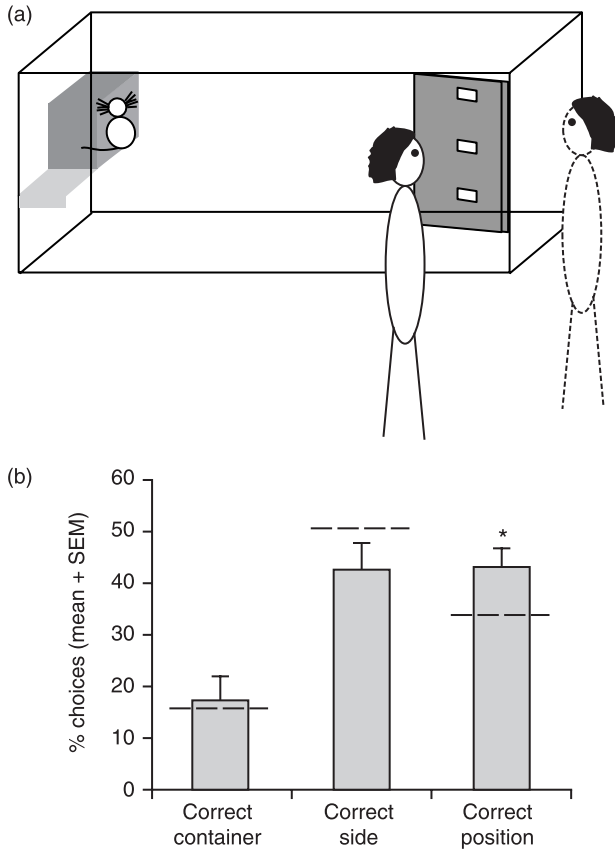
Figure 6.2 (a) An alternative setting for testing common marmosets' understanding of visual perspective. A human experimenter indicates with her gaze which of six containers is baited. To identify the baited container, marmosets have (1) to extrapolate the line of sight of the human experimenter, but also (2) to understand that her gaze cannot penetrate the wooden board. (b) Results show that marmosets choose the correct position more often than by chance, but not the correct side of the board (dotted lines: chance levels). This indicates that they do not understand that gaze cannot penetrate an opaque object, even though they extrapolate the line of sight.

individuals' visual perspective in one study, they failed to do so in the second study. There are two plausible explanations for these conflicting results. The first is that common marmosets do understand visual perspective but that they were not able to deploy this ability in the specific context of the second study. The ecological validity of the second study was low, indeed, where the marmosets were required to use a human experimenter's gaze. However, the same argument would apply to the previous findings in the object choice task (Burkart & Heschl, 2006) where the same subjects had been tested

successfully with a very similar experimental setting that differed only in the arrangement of the containers.

The second explanation is that marmosets are not able to understand visual access but somehow managed to solve the competition setting differently, using an alternative mechanism. Such an alternative mechanism could consist in the animals first following the gaze of the dominant competitor in the compartment opposite to the freely visible piece of food. Because the dominant individuals could only see one piece of food, they could always look only at this piece of food. If the subordinate subsequently treated the piece of food viewed by the dominant as already belonging to the dominant, it would avoid it. Hence, it would choose the hidden one by default, not because it was invisible to the dominant subject.

Gaze following is well demonstrated for common marmosets (Burkart & Heschl, 2006), but the second step of this alternative mechanism, i.e., that marmosets treat a piece of food that is stared at as already belonging to the looker, needs to be demonstrated. To do so, we ran a very easy learning experiment with two groups of completely naïve marmosets. Each marmoset had the choice between two pieces of food: one that was directly looked at by a human experimenter and one that was not looked at. Marmosets from one group were allowed to take the piece of food that was directly stared at, while marmosets from the other group were allowed to take the piece of food that was not stared at. If marmosets had a disposition to treat a stared-at piece of food as already belonging to the looker, the learning task should be much easier for the second group and this was indeed the case (Figure 6.3). Therefore, the hypothesized alternative mechanism for solving the competition setting could actually be at work. Furthermore, a qualitative reanalysis of the marmosets' behaviour during the food-competition task revealed that their looking patterns were also consistent with this alternative mechanism.

In sum, the results suggest that even though common marmosets behave very skilfully in sociocognitive contexts, there is no unambiguous evidence so far that they possess a Theory of Mind or simple precursors to it.

HOW CAN COOPERATIVE BREEDING ENHANCE COGNITIVE PERFORMANCE?

Accumulating evidence indicates that cooperative breeding and enhanced cognitive performance are indeed linked in nonhuman primates. However, it is less clear how this effect is mediated on a mechanistic level: whether certain aspects of cooperative breeding systems are responsible for the increase in cognitive performance rather than others, and if so, which ones. We also need to understand how these aspects interact to finally constitute the functional pathways that lead from cooperative breeding to enhanced cognitive performance. I will try to identify and explore such potential pathways and evaluate them by assessing their explanatory power with regard to those
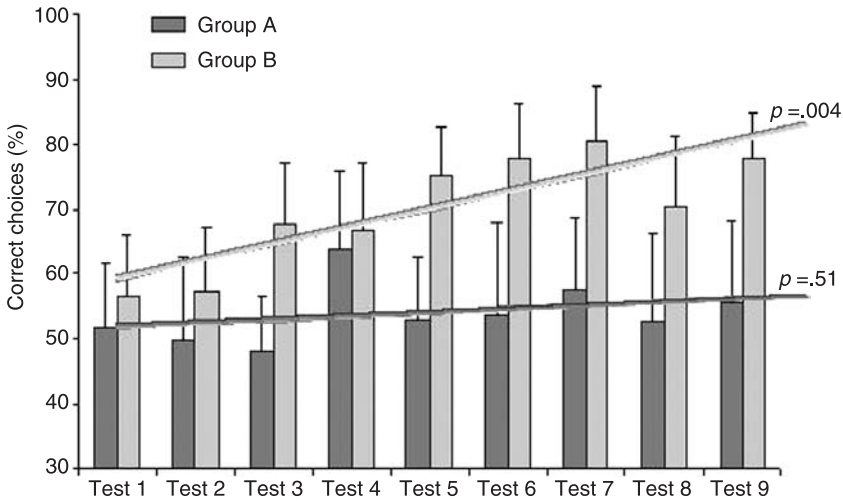
Figure 6.3 Results from the learning experiment indicating that marmosets have a disposition to treat a gaze as a claim. The performance of Group A, who were learning to take a piece of food that was directly stared at, increased over time, while the performance of Group B, who were learning to take a piece of food that was not directly stared at, did not.

sociocognitive domains where cooperatively breeding primates seem to excel. Unfortunately, little research has been devoted to comparing cognitive abilities and performance between cooperatively and noncooperatively breeding primates systematically across domains; thus, important differences in some domains may be overlooked or similarities in others incorrectly inferred. The potential pathways outlined here must therefore be considered tentative. However, such a sketch may prove useful in generating testable predictions about the cognitive domains in which differences between cooperatively and noncooperatively breeding primates can be expected.

A first distinction I will draw is between direct and indirect effects of cooperative breeding on cognitive performance, where direct effects are associated with immediate behavioural requirements of the cooperative breeding system. Indirect effects, on the other hand, are those mediated through noncognitive consequences of cooperative breeding, e.g., increased social tolerance, altered motivational predispositions, or decelerated ontogenetic development.

Direct influences of cooperative breeding on cognitive performance

In cooperative breeding systems of callithrichids, immediate behavioural requirements thought to influence cognitive functioning include the transfer of infants from one caregiver to the next, the coordination and alternation of

vigilance duties, group defence and caregiving activities among group members, and food sharing.

A consequence of multiple caregivers' involvement in child carrying is that callithrichids frequently have to transfer infants from one caregiver to another. This occurs in the canopy and requires high levels of behavioural coordination, because failed attempts may result in infants falling down and dying. Likewise, turn taking in vigilance activities and communal group defence also require close behavioural coordination, which in turn might prime callithrichids for other cooperative activities, e.g., cooperative problem solving in experimental settings. In order to successfully coordinate behaviour with another individual, both in time and space, it is necessary to pay close attention to the other individual's activities. The propensity to carefully monitor the signals and behaviours of others might explain why tamarins in comparison to other nonhuman primates socially learn to avoid noxious foods by observing spontaneously occurring disgust reactions from conspecifics sampling unpalatable food, as pointed out by the authors of that study (Snowdon & Boe, 2003). The difference from other monkeys in socially learning food aversions therefore would rather lie in a lack of monitoring the spontaneous behaviours of others, than, e.g., in knowledgeable tamarins intentionally producing signals influencing their group members' behaviours. Furthermore, the mutual need for accurate behavioural coordination might also provide the context for developing more complex forms of vocal communication (Snowdon, 2001b), perhaps simply by increasing the salience of certain types of crucial behaviours through accompanying vocalizations.

Another important behavioural component of callithrichid breeding systems is food sharing. Food sharing not only takes the form of tolerated theft but also of active food offering, predominantly to immatures. Typically, actively shared food items are highly preferred items like insects. There are indications that food offering is not a completely hardwired response automatically triggered whenever a prized food item is encountered in the presence of immatures, because the adult has at least some control over food sharing events. Offering food requires from the donor the ability to inhibit the prepotent action tendency to eat the food item by itself. Hence, we would expect that cooperative breeding also improves inhibitory control in callithrichids via food offering. In a reversed contingency task, however, in which subjects have to reach for a smaller amount of food in order to receive a larger amount (and therefore must inhibit the prepotent action tendency to reach for the larger amount of food), cotton-top tamarins performed no better than other monkeys (Kralik, Hauser, & Zimlicki, 2002).

Indirect influences of cooperative breeding on cognitive performance

In contrast to direct influences, indirect influences of cooperative breeding are thought to enhance cognitive functioning mediated by noncognitive

consequences of cooperative breeding, such as increased social tolerance, altered motivational predispositions towards prosocial other-regarding preferences, and information donation in the form of teaching and decelerated ontogenetic development. Here I will only develop the effect of increased social tolerance on visual perspective taking.

Within groups of cooperatively breeding primates, social relationships are very strong and characterized through high rates of affiliation and tolerance (Aureli & Schaffner, 2006). The role of social tolerance for social learning performance has been addressed by Coussi-Korbel and Fragaszy (1995), who developed a well-confirmed model relating social learning to social dynamics among group members. Hence, the increased social tolerance associated with cooperative breeding has the potential to increase social learning performance without adding qualitatively new cognitive abilities.

Common marmosets' behaviour in the perspective-taking tasks can also be reconsidered in terms of increased social tolerance. The proposed alternative mechanism, which explains why marmosets passed the competition setting, consists of first following the gaze of the dominant individual in the opposite compartment and then avoiding the piece of food the dominant was looking at. Both simple gaze following and treating a gaze as a claim seem to be present in other nonhuman primates as well, if tested separately. Simple gaze following has been demonstrated in a wide range of nonhuman primates (reviewed in Emery, 2000), and at least olive baboons (Vick & Anderson, 2003) and rhesus macaques treat a gaze as a claim (Flombaum & Santos, 2005). What might be the role of cooperative breeding? First, social tolerance may have facilitated the decision of subordinates to enter the middle compartment at all. Even subordinate marmosets with their very high levels of social tolerance sometimes were reluctant to do so, despite being given a small headstart. It is conceivable that more competitive species face even higher motivational thresholds. Second, as discussed earlier, the signals of conspecifics tend to be more carefully monitored in cooperative breeders. Subordinate individuals of less tolerant species no doubt must monitor their conspecifics as well, because they continuously risk being attacked if they interfere with others' interests. However, their main concern must be: "Am I likely to be aggressed or not?", a concern likely to overshadow other aspects. In addition, the fact that in most primates a direct gaze is usually perceived as a threat makes it more difficult for them to monitor conspecifics' gazing behaviours. In contrast, marmosets do not seem to perceive a direct gaze as a threat in the same way that other primates do, as mirrored in remarkably low levels of gaze aversion (de Wandelaer & Burkart, 2008). Such a relaxed attitude towards directed gaze may also explain why it is fairly easy to evoke the use of experimenter-given gaze cues in object choice tasks, including eye-only cues, in tamarins (Neiworth, Burman, Basile, & Lickteig, 2002) and marmosets (Burkart & Heschl, 2006).

Finally, if cooperative breeding leads immatures to develop at a slower pace than if the mothers were solely responsible for rearing them, as recently

suggested (Hrdy, 2005a; Kramer, 2005; Langen, 2000), then we can expect a suite of further indirect cognitive consequences of cooperative breeding. Delayed maturation provides infants and juveniles with more opportunities for learning in "protected environments", i.e., while still being provided with food and shelter by others and not being responsible for predator detection. Thus, the amount of both individual and social learning experiences can be amplified through the increased availability of time during the extended juvenile period and through the presence of multiple, highly tolerant role models. In addition, the constellation of frequent social learning situations and the presence of multiple role models also offers further conditions conducive to the emergence of simple forms of teaching.

IMPLICATIONS FOR HUMANS

Are humans cooperative breeders?

Many researchers have confirmed that humans can be considered cooperative breeders (Foster & Ratnieks, 2005; Hrdy, 2005b; Kramer, 2005; Mace & Sear, 2005). Most importantly, in humans individuals other than the genetic parents are involved in childcare, e.g., older siblings, aunts, and uncles, or even unrelated individuals, but perhaps grandmothers play the most important role. Compared to great apes, who give birth to the next offspring only after 5–9 years (Knott, 2001), i.e., when the previous offspring has reached independence, birth intervals in typical hunter-gatherer societies are usually about 3–4 years. A human 4-year-old is far from independent and it will take her about 10 more years to become so. Thus, humans show both short birth intervals and slow maturation of offspring. Finally, human mothers also show conditional investment in their offspring, depending on the perceived available allomaternal support (Hrdy, 1999). For example, teenage mothers are more likely to provide adequate care the more social support is subjectively available to them, usually in the form of the father and grandmothers of the child (Hashima & Amato, 1994; Leahy Warren, 2005). In sum, there is good overall evidence that our ancestors became cooperative breeders after they split from the great ape lineage. Can we conclude on the basis of what we know from other cooperatively breeding primates that this breeding system might have influenced our own cognitive abilities?

Did cooperative breeding influence our cognitive abilities—and how?

If we maintain the distinction between direct and indirect influences of cooperative breeding on cognitive performance, we first must identify the immediate behavioural requirements arising from the human cooperative breeding system. Presumably these behavioural requirements do not differ

significantly compared to callithrichids; they include close behavioural coordination associated with infant and child care and the coordination of different activities between group members, both leading to enhanced monitoring of others' signals and behaviours. Likewise, indirect effects might also be mediated through similar functional pathways as in callithrichids, i.e., via social tolerance resulting in altered attentional structures with regard to both targets and allocation of time, in enhanced social learning and in opportunities for even closer behavioural monitoring, via emerging prosocial motivational predispositions and via decelerated ontogenetic development.

Analyses of the unexpected sociocognitive performances of callithrichids revealed that they tend to be based on a slightly different use of abilities that are also present in other monkeys, rather then being a consequence of completely new and more complex cognitive abilities, and the same might be true for humans: The crucial difference between callithrichids and humans may not pertain to the ways in which cooperative breeding affects cognitive functioning, but rather to the preexisting cognitive substrate on which the selective pressures of the breeding system were acting. At this point, we can return to the traditional comparative approach, which tries to delineate the characteristics of evolutionary ancestors explicitly. Pinning down exactly when cooperative breeding arose during our evolutionary past is a difficult task. However, it must have occurred somewhere after the origin of hominins, because with the exception of humans, none of the extant apes breeds cooperatively. Therefore, a conservative measure for assessing the minimal cognitive equipment on which cooperative breeding was acting with certainty is to use the modal cognitive skill set of the extant great apes as a point of reference.

While the gap in cognitive ability between monkeys and apes is less pronounced than one might expect (Tomasello & Call, 1997), there are nonetheless important differences both in the wild and in captivity. For example, apes are more proficient tool users than monkeys (Visalberghi, 1997) and show simple forms of planning for the future (Mulcahy & Call, 2006). In the sociocognitive domain only apes are able to recognize themselves in a mirror (Gallup, Anderson, & Shillito, 2002) and their observational social learning abilities clearly go beyond those of monkeys, including marmosets (Caldwell & Whiten, 2002; Horner & Whiten, 2005). Finally, as discussed previously, there is now increasing evidence that they possess some simple Theory of Mind abilities such as an understanding that actions are intentional and goal-directed (Call & Carpenter, 2002) or an understanding of perceptions (Bräuer, Call, & Tomasello, 2005; Shillito, Shumaker, Gallup, & Beck, 2005; Tomasello et al., 2003). These Theory of Mind abilities in apes are mainly deployed in competitive situations, one reason why it took researchers so long to demonstrate them.

Thus, we may surmise that the cognitive abilities already in place became available in new combinations and new contexts as a consequence of cooperative breeding. For example, simple planning abilities in food-related activities such as tool use would greatly improve the coordination of activities

between group members, and sophisticated forms of social learning that already existed would get a further boost through enhanced social tolerance. The most drastic effects, however, may have issued from the new opportunity to use Theory of Mind abilities in cooperative contexts, with prosocial motivational predispositions playing key role for this transition.

So far the cognitive consequences of cooperative breeding have been discussed from the perspective of mothers and allomothers, but other authors have emphasized the perspective of infants and children (Chisholm, 2003; Hrdy, 2005a). If maternal investment is conditional, children should try hard to engage mothers and allomothers to invest in them. This becomes particularly important when the arrival of younger siblings further reduces the amount of investment from their mothers, at around 4 years of age. In line with this argument, 4 years is exactly the age at which human children have acquired a basic, full-fledged Theory of Mind, allowing them to better understand and also manipulate the intentions of potential allomothers. Fu and Lee (2007) showed that children start to show flattering behaviour at around the same age. A detailed analysis of 6-year-olds further revealed that they are inclined to flatter familiar adults and familiar children as well as unfamiliar adults, but not unfamiliar children, i.e., individuals to whom they have social bonds or who potentially serve as allomothers.

In sum, cooperative breeding acting on an ape-like brain in a first step might have allowed our ancestors to use their already sophisticated cognitive abilities in new contexts. This would be particularly true for the emerging Theory of Mind abilities. Over time the greater advantages of slightly better Theory of Mind abilities for our ancestors in comparison to noncooperatively breeding hominids, could have played an important role in the evolution of our full-fledged Theory of Mind. Given that Theory of Mind is strongly associated with executive functions (Perner et al., 2003), which in turn are among the main ingredients of general cognitive ability in humans (Gray & Thompson, 2004), cooperative breeding in humans might even be linked to our cognitive abilities in a much more general way than would be expected at first sight.

CONCLUSIONS

Looking at animals in order to understand exclusively human properties seems counterintuitive. Nevertheless, there are at least two ways to do so. However, rather than refining our knowledge on these properties per se, looking at animals can complement this knowledge by informing us about the evolutionary origins of exclusively human properties. Besides the traditional comparative approach, a second way consists of identifying general principles and regularities between the occurrence of environmental constellations and reliably associated consequences in animals, which also may have had an impact for human evolution. The present chapter exemplifies this

second approach using the case of cooperative breeding. In nonhuman primates cooperative breeding seems to be associated with enhanced cognitive performance, especially in the social context. However, cognitive mechanisms underlying a given surface performance are not necessarily the same, and fine-grained analyses are needed to reveal these mechanisms. Such an analysis of the understanding of visual perspective in common marmosets suggests that their enhanced cognitive performance is not the result of completely newly emerged cognitive abilities. Rather, it seems to arise from the deployment of already existing abilities in different contexts and in different combinations. The depiction of potential pathways that lead from cooperative breeding to enhanced cognitive performance indicate that the same seems to be true for other extraordinarily skilful social behaviours in cooperatively breeding primates as well.

Hence, the effect of cooperative breeding on cognitive performance strongly depends on the starting point, the cognitive equipment of a species which adopts the cooperative breeding system. In the case of humans, this was at least equivalent to the cognitive abilities of the last common ancestor that we shared with other great apes, which can be delineated using the traditional comparative approach. Following the same functional pathways as in other cooperative breeding primates, this breeding system might in a first step have made available already existent abilities in different ways and in different contexts. This is most intriguing with regard to simple Theory of Mind abilities that supposedly were already in place but mainly used in competitive contexts. The effect of cooperative breeding then might have been that these abilities became available in other contexts as well, especially in cooperative and prosocial ones. Compared to other lineages that stayed within the traditional great ape breeding system, this amplified the advantages of slightly better functioning Theory of Mind abilities, favouring the evolution of a fully fledged Theory of Mind as a uniquely human feature. At the same time, with prolonged juvenile periods already in place, some of the costs necessary for developing the bigger brains necessary were already paid in advance, playing a further facilitating role. Finally, due to the reliance of a fully fledged Theory of Mind on executive functions that also play a crucial role for our general cognitive ability, cooperative breeding might have had particularly far-reaching consequences in our species.

Obviously, the sketch of the effects of cooperative breeding on cognitive abilities presented in this chapter is still incomplete and further research is still needed. Nevertheless, pursuing this line of thought both theoretically and empirically holds the potential to provide essential insights into human traits given the far-reaching consequences the cooperative breeding system seems to have had during human evolution.

7 Attentiveness toward others and social learning in domestic dogs

Zsófia Virányi, Friederike Range, and Ludwig Huber

Social complexity and the evolution of cognition (the "social intelligence hypothesis"), language, and culture are likely to be closely linked. To achieve and maintain a complex social system, individuals must employ numerous cognitive and physiological control mechanisms in order to develop and nurture social relationships. However, in order to interact with other individuals and to learn from them it is necessary to pay *attention* to them to gain information. The processes of attention towards other group members and means of learning by observation in human and nonhuman animals are the focus of this chapter.

Recent evidence from ethology and neurobiology suggests a surprising degree of convergence in social organization and cognitive abilities among the social vertebrates. However, this convergence in particular abilities is often based on divergent, conserved traits. Evolution by means of natural selection is generally a conservative process that preserves adaptations that work as long as possible. For instance, sociocognitive traits are based on a number of conservatively maintained structural and physiological components—emotional systems, bonding mechanisms in the brain, the sympathico-adrenergic and the hypothalamic-pituitary-adrenal axes for coping with stress, as well as on common principles for the social modulation of steroid hormones.

Humans are not exceptions to these evolutionary trends, but they appear to have selectively strengthened several important cognitive abilities in the social domain, such as joint intention and attention, ostensive-communicative processes, imitation, teaching, and perspective taking. Thus, human cognition is not unique, but a specific (in the literal meaning of the word) instance of primate, mammalian, or vertebrate cognition. As emphasized by Tomasello (2000), human cognition is not just *similar* to nonhuman primate cognition, it is *identical* with respect to many of its structures. Thus, Tomasello concludes that the study of primate cognition should play a more important role in cognitive science than it has previously.

However, we do not know whether some human cognitive traits might have undergone a much more recent, hominoid development and are therefore not exhibited by our nearest primate relatives. In order to better understand the

possible selective forces behind such capabilities, one needs to study a nonprimate control group.

In recent years dogs have perhaps represented the best model of all possible control species (Miklósi, Topál, & Csányi, 2004). In fact, the intense research focus on dogs' social interactions and communicative skills over the last decade has shown that they are extremely skilled at reading human social and communicative behaviour. These unusual social skills probably evolved during domestication. In the process of domestication some aspects of dogs' social-cognitive abilities have converged—within the phylogenetic constraints of the species—with those of humans through a phylogenetic process of "enculturation". This process may be similar in some respects to the onto-genetic process of enculturation experienced by nonhuman primates raised by humans (Hare & Tomasello, 2005).

Imitation, gaze following, and perspective taking are crucial components of cultural learning. All of these abilities have been found in nonhuman animals, not only in great apes, but also in such diverse species as marmosets (Voelkl & Huber, 2000, 2007) and ravens (Heinrich & Bugnyar, 2007). Going a step further, several developmental psychologists have proposed that humans' ability to participate with others in collaborative activities with shared goals and intentions is a key factor in cultural learning (Tomasello et al., 2005). The sometimes extremely close relationship between dogs and their owners may provide a basis for similar processes of shared attention and intentionality to emerge. This suggests a number of questions for research. For example, if dogs really are skilled at reading human social and communi-cative behaviour, do they understand humans' behaviour in terms of pursued goals or underlying intentions? Or, would dogs, like human children (Gergely, Bekkering, & Király, 2002), selectively reenact a demonstrated action on the basis of inferential processes? This chapter addresses these questions by reviewing and discussing the evidence on attention in dogs and concludes with remarks on the significance of studies on dogs for cognitive science.

ATTENTIVENESS TOWARDS OTHERS

In social species one of the crucial sources of information is the behaviour and interactions of group mates. Paying attention to companions and monitoring their behaviour enables individuals to make better decisions when engaging in cooperative or competitive social interactions, when responding to social or physical changes in the environment. Attention is obviously required for communication as well as for learning from others. Since dogs have a complex social life, they can profit from paying attention to their companions in diffe-rent situations. Moreover, living in mixed human-dog groups, dogs need to deal with both conspecific and human companions. Thus, in order to under-stand domestic dogs' social learning abilities, their social attentiveness towards other dogs and towards humans should be investigated in parallel.

Social attentiveness as a species characteristic

Like their closest wild relatives, domestic dog groups are usually assumed to have a social life comparable to that of wolf packs. There are, however, group activities like cooperative hunting or the raising of pups in which spontaneously formed dog groups perform more poorly than wolf packs (Boitani & Ciucci, 1995). This suggests that they lack the social structure and coordinated activities of wolf packs. As a consequence, it is possible that domestic dogs pay less attention to their conspecifics than wolves do. Unfortunately, however, direct wolf–dog comparisons of attentiveness towards conspecifics are not available.

Probably due to their history of domestication, many studies have investigated the species-specific features of dogs' attentiveness towards humans. In a comparative project, Hungarian researchers hand-raised dogs and wolves identically in order to give them the same extensive experience with the human environment. In spite of the identical upbringing and training history of both groups, the dogs showed increased readiness to look at humans in various situations. When facing an unsolvable problem, dogs looked at their owners sooner than the wolves, which continued to try to solve the problem on their own (Miklósi et al., 2003). Similar differences were observed at a very early age when the frequency of looking at the owner's face and other communicative behaviours were measured in a slightly stressful situation (Gácsi et al., 2005). Moreover, in a two-way choice task the experimenter needed a longer period of time and had to call the wolves more times than the dogs in order to gain their attention before pointing to the location of the food (see Figure 7.1 later) (Virányi et al., 2008).

Based on these results, it seems that dogs' attentiveness towards humans has increased over the course of domestication. It is still unknown to what extent this human-directed attention is based on a generalization of interest from conspecifics to human companions (Hare & Tomasello, 2005) or whether it reflects some novel characteristic of dogs. Comparable analyses between wolf–wolf and dog–human interactions should reveal whether the form or the degree of dogs' attention towards humans goes beyond the attention wolves pay to their conspecifics. However, it is plausible that at a certain stage of domestication dogs were directly selected for higher attentiveness (Miklósi et al., 2003). Alternatively, it might be a capability indirectly influenced by selecting for other features. For example, dogs' increased attachment to humans compared to even young wolves (Topál et al., 2005) may be accompanied by higher attentiveness towards humans. There is likely no direct functional relationship between puppy–mother attachment in wolves and the life-long attachment between a dog and its owner. Rather, dogs seem to have evolved a special capacity for attachment to humans. If dogs' dependency on humans is the basis for their attentiveness, then the latter can be considered a novel, human-directed characteristic, which does not originate from wolves' conspecific-directed behaviour alone.

Social relationships and social attentiveness

The connection between animals' attentiveness towards certain individuals and their personal relationships is supported by several studies. In primate groups, for example, visual attention between group members is systematically related to dominance status (McNelis & Boatright-Horowitz, 1998) and looking at others has been employed as a direct measure of social interest (Moore, Cleland, & McGrew, 1991). Similarly, in a series of experimental studies applying the two-hole procedure (see later), the subjects' gazing behaviour was measured directly. Marmosets were found to look longer at conspecifics of the opposite sex (Range & Huber, 2007), whereas children and juvenile keas watched peers longer than adult conspecifics (Range, Horn, Bugnyar, Gajdon, & Huber, in press). Differential attentiveness to conspecifics of different age, sex, dominance rank, and familiarity might also explain why these factors influence the readiness of animals to socially learn from one another (Nicol & Pope, 1994; Nishida, 1987; Swaney, Kendal, Capon, Brown, & Laland, 2001; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996). Coussi-Korbel and Fragaszy (1995) suggest that in egalitarian (tolerant) social systems higher attention and information transmission may be expected among all group members than is the case in more despotic, less tolerant, systems due to closer proximity and more tolerant relationships between individuals. However, this would also suggest that the identity of the demonstrator might influence observational learning less in more egalitarian species than in despotic species.

Domestic dogs live in a tolerant social system both in relation to conspecifics and to humans. In comparison with wolves, dogs show reduced aggression, increased playfulness, and other pedomorphic features (Goodwin, Bradshaw, & Wickens, 1997), which may be conducive to more relaxed, tolerant relationships and interactions with (even unfamiliar) conspecifics. Notably, humans describe their attitudes towards dogs mainly with affective terms (Topál, Miklósi, & Csányi, 1997) and dogs often have a child status in the family (Topál, Miklósi, Csányi, & Dóka, 1998), suggesting also a tolerant social environment. Coussi-Korbel and Fragaszy's (1995) hypothesis predicts that in such a tolerant social system the identity of a demonstrator should have little influence on the attention paid towards her/him. However, the extent to which dogs' relationships to humans and to other dogs are comparable and whether they provoke a similar attention span must be investigated.

To examine this question we applied the two-hole procedure mentioned earlier to measure attention in adult pet dogs (Range et al., in press). The dogs were separated from a conspecific or a human model by an opaque screen with two holes, which only allowed visual access to the activities of the demonstrator on the other side. The model was trained (dogs) or instructed (humans) to search for a tightly crumbled piece of paper buried in a box of wood chips, rip the paper apart, and then chew the reward hidden inside. If the dogs wanted to see what the model was doing, they had to come to one of

the holes, which allowed us to determine exactly how often and how long they watched the model. We assigned the dogs randomly to the two experimental groups: human demonstrator or dog demonstrator. Within the human demonstrator group, each subject ($n = 20$) was tested twice—once with its owner and once with a nonfamiliar human as model. In the dog demonstrator group, each subject ($n = 18$) was tested with a female and a male demonstrator dog as the model. We found that overall observers paid more attention to the human demonstrator (18% observation time) than to the dog demonstrator (7.7% observation time). Dogs looked for a longer duration in the case of a human demonstrator but not more often, which means that a human could hold the attention of the dogs longer than a conspecific. Since little is known about whether the subjects' experiences with humans and with other dogs are comparable in food-manipulating and eating situations, this preference for watching humans can be explained either by the domestication history of dogs or by learning processes.

Interestingly, the time spent watching a dog demonstrator was not influenced by the sex of the model. Even more surprisingly, dogs did not pay significantly more attention to their owners than to a stranger. The finding that dogs' attentiveness to humans and ability to learn from humans are not necessarily affected by the identity of the human demonstrator receives further support from a detour task, where dogs learned with the same efficiency from a stranger as from their owner (Pongrácz et al., 2001; Pongrácz, Miklósi, Tímár-Geng, & Csányi, 2004). These results confirm the hypothesis that the dogs' social environment is tolerant enough to allow close observation of both humans and dogs independent of their identity. Further studies are needed, however, to test whether the dominance or the familiarity of a dog demonstrator influences the dogs' attentiveness and to determine to what extent the identity independence of learning from humans depends on the context of the observation and the method of demonstration.

Attentiveness as an individual characteristic

Both the direct and the broader context of a particular situation can strongly influence the attentiveness as well as the general activity of animals (Alberts, 1994). It has been shown that attentiveness in dogs changes with age (Neilson, Hart, Cliff, & Ruehl, 2001; Vas, Topál, Péch, & Miklósi, 2007) and training level (Vas et al., 2007). Moreover, it is influenced by the housing conditions, the timing of testing, as well as the novelty of the environment (Neilson et al., 2001; Tobler & Sigg, 1986). It also depends on the immediately preceding events, e.g., dogs show higher obedient attentiveness to a person after playing with her (Rooney & Bradshaw, 2002). Nevertheless, there are recognizable differences among individual dogs in their attentiveness-impulsivity/activity that is often described as a personality trait (Riese, 1987).

In human children attention deficit hyperactivity disorder (ADHD) is characterized by problems in attention skills and by abnormal motor behaviour

(e.g., Gittelman, Mannuzza, Shenker, & Bonagura, 1985). Using simple behavioural tests, different levels of activity and learning abilities have also been observed in dogs (Corson, et al., 1980). Moreover, a recent study has shown that the application of a human ADHD questionnaire, developed to study children's symptoms, is a reliable and valid method of assessing attention and activity in dogs (Vas et al., 2007). Based on the questionnaires completed by owners, two subscales were defined: inattention and activity-impulsivity. These can be regarded as unrelated dimensions of pet dogs' behaviour which seem to be functionally analogous to the phenotypic manifestation of ADHD that involves more or less independently varying degrees of attentional and motor deficits (Huang-Pollock & Nigg, 2003).

ATTENTIVENESS AND SOCIAL LEARNING

Social attention is important for species that live in groups for several reasons. First, watching others may provide important information about their physiological or social status, e.g., reproductive receptivity, their expected behaviour, e.g., when they are about to attack, or their relationships, e.g., relatedness, dominance. Hence, it may help the observer develop adaptive behaviour in the given situation and on future occasions. Rooney and Bradshaw (2006) found that whether dogs approach a dog–human pair depended on the previously observed activity of the pair. If competition over an object by the human–dog pair was preceded by play signals performed by the human, the observer dogs approached the winner of the game first. When the game was replaced with a contest between the human and her dog, the observer dogs were slower to approach either member of the pair, suggesting that participants in a competitive interaction are less desirable social partners than the participants of a game.

Second, paying attention to companions may provide information about the environment, e.g., where to find food, where to expect a predator, etc. In a longitudinal study involving object choice tests (Virányi et al., 2008), dogs and wolves had the opportunity to locate a food reward by attending to the experimenter's pointing gesture. In the first 20 trials it took the experimenter a long time to make eye contact with the wolves and the wolves randomly chose one of the two hiding places. However, after 7 months of training the latency for obtaining eye contact with the wolves decreased to the level typical of dogs and the wolves also became successful in following the pointing gesture (Figure 7.1). These parallel changes may be interpreted as indicating that the wolves learned to pay attention to the pointing experimenter, which also helped them use the pointing gesture to find the food.

Third, watching others is clearly necessary to learn something from them in the sense that knowledge acquired by observation can be applied later on. In human research studies show that after observing a particular demonstration, infants can successfully solve the same problem themselves when tested
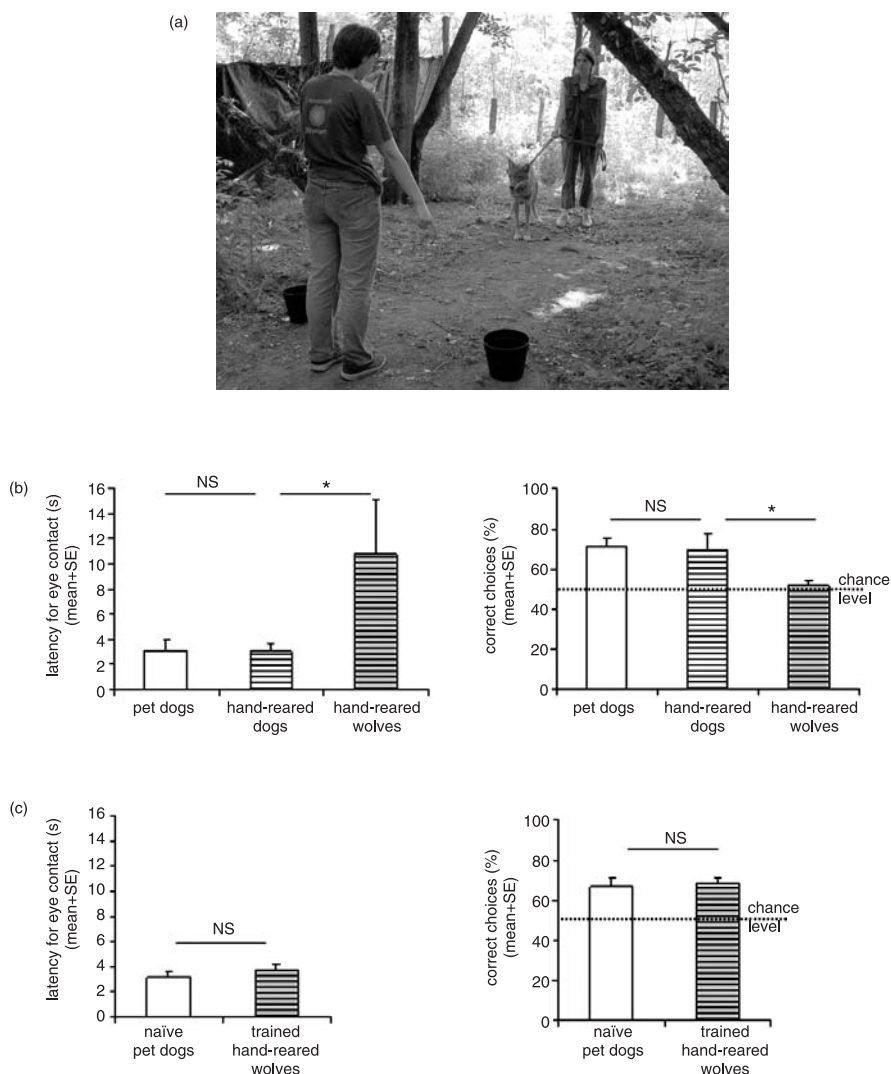
Figure 7.1 (a) Object-choice task for hand-raised wolves and for dogs. One of the two containers is baited with food. The experimenter first calls the subject's attention and then, when eye contact is formed, points to the location of the food. After she withdraws her hand the subject is allowed to choose one container. (b) Latency of forming eye contact with the experimenter (left) and the percentage of choosing the baited container (out of 20 trials) (right) at the age of 4 months in pet dogs, hand-reared dogs, and hand-reared wolves. (c) Latency of forming eye contact with the experimenter (left) and the percentage of choosing the baited container (out of 20 trials) (right) in 11-month-old animals. In this case the hand-raised wolves—after being tested in 100–400 different pointing trials over 7 months—were compared to naïve pet dogs that were tested with the pointing gesture for the first time.

a week later (deferred imitation; Meltzoff, 1995) or in another context (Learmonth, Lamberth, & Rovee-Collier, 2005). Dogs also show social learning abilities, but they are usually tested immediately after the demonstration, at the same location, and in the presence of the same participants. Consequently, it is not known how long their acquired knowledge persists and whether it can be generalized. Nevertheless, dog pups can learn via repeated observation of their mothers to locate and retrieve a sachet of odour-producing narcotic between the ages of 6 and 12 weeks (Slabbert & Rasa, 1997). These pups performed better than nonexposed pups when tested 3 months later without further reinforcement during the interim period.

Attention at the behavioural level

With regard to social learning, it is important to note that an individual can only learn socially from another if it actually pays attention to the demonstration. There are two attention processes in humans (Cohen, 1972) that might also be important for the study of social learning in nonhuman animals. An attention-getting process determines whether the subject will turn to look at a stimulus. An attention-holding process, on the other hand, determines how long the subject will continue to gaze at the stimulus once it has looked. With regard to social learning tasks, it is likely that the frequency and the duration of the observer's glances towards a demonstration influence the type of information that can be extracted about the task at hand. If an observer briefly looks a few times during a demonstration, the observer might be able to extract enough information for stimulus enhancement to occur, but not for imitation. For example, in a detour task differences among breeds were found regarding the number of looks towards the owner when the experimenter was demonstrating how to detour around the fence. However, later performance did not differ among breeds (Pongrácz, Miklósi, Vida, & Csányi, 2005). Thus, it seems that looking back at the owner during the demonstration did not prevent the dogs from extracting the necessary information from the demonstrator's action. This is probably because they only needed to complete the trajectory of the demonstrator's movement around the fence. However, in complex demonstrations such as action sequences or actions that are not part of the observer's behavioural repertoire, attending continuously to the demonstrator's action may be necessary and the duration of looking towards the model may be more important than the frequency of looks (Range & Huber, 2007). Moreover, the duration of looking must itself be of sufficient length for the observer to perceive the complete act in order to copy it; a somewhat longer duration is required for more complicated and novel actions (Miklósi, 1999).

In social learning studies the frequency of looking away from the model (Pongrácz et al., 2004), the duration of looking at the demonstrator (Pongrácz et al., 2004), and the number of looks at the source of information (Campbell & Namy, 2003) have been used to describe the observers' attention at the

behavioural level. However, it is undeniable that attention has other "invisible", cognitive and motivational components as well. Identical behavioural symptoms, therefore, may accompany different attentional states in terms of the level of (cognitive) attentiveness or the precise focus of attention. Even in such a simple situation as showing a dog its favourite ball, strong and stable individual differences can be found in the heart rate variability of the animals (Maros, Dóka, & Miklósi, 2008). Although at the behavioural level all dogs showed the same attentiveness (looking at the ball continuously with erected ears while sitting still and alert), the heart rate increased in some, but decreased in others. The authors suggested that the latter were waiting for a request to perform a certain task before being allowed to play with the ball (probably accompanied by increased anticipation), whereas the dogs with an increase in heart rate prepared themselves for play causing overall excitement.

Attention at the cognitive level

It is difficult to describe cognitive attentiveness without relying on physiological measures or observers' verbal reports. Success in solving specific problems after observing others indicates attentiveness during the demonstration, but this criterion would be obviously circular, if the aim is to describe the level of attention underlying social learning. Moreover, acknowledging a model's actions does not necessarily lead automatically to reenacting them. The decision whether or not to copy another's behaviour may depend on additional processes ranging from reacting to contextual cues (Learmonth et al., 2005) to applying other inferential processes (Gergely et al., 2002). Therefore, the performance on social learning tasks may underestimate the observers' attentiveness. In sum, paying sufficient attention to a model is a prerequisite for social learning, but it does not necessarily lead to copying the behaviour.

Several studies have demonstrated that producing the observed action may depend on the conditions of the demonstration. Akins and Zentall (1998), for example, found that Japanese quails copied a model's method only if the model was rewarded for its activities. A study of human infants showed that their symbol learning depended on whether the production of the symbol was contingent on the experimenter's giving social-referential cues (Campbell & Namy, 2003). Although the attentiveness was behaviourally described as identical in the different conditions, the level and focus of the observers' attention may have varied and produced the results in turn, which would then not necessarily reflect additional cognitive processes.

In one of our studies, however, the data clearly showed that members of the different experimental groups did pay attention to the same components of the demonstration, but still reenacted it selectively, reflecting additional inferential processes. Based on the intriguing results of Gergely and his colleagues (2002), which showed that 14-month-old children copy a nonpreferred action only if the model has the opportunity to use the preferred action to solve the same problem, but do not copy it if constraints "force" the model

to avoid the preferred action, we investigated dogs' behaviour in a comparable task. We designed a manipulative task that required the dogs to pull down a wooden rod to open a food container connected to the rod in order to gain a food reward (Range et al., 2007). Manipulations of the dogs in the control group ($n = 14$) that had not seen a demonstration of the task, showed that the dogs' preferred method to solve this problem is pushing the wooden rod down with their mouth.

In two experimental groups we let other dogs observe an adult female dog that used her paw to obtain food from the apparatus. In one group the demonstrator dog's use of this nonpreferred method was explicable because she was carrying a ball in her mouth (mouth-occupied group, $n = 21$), while in the second group no constraints were present to explain the demonstrator's choice of the nonpreferred method (mouth-free group, $n = 19$). The dogs in the two experimental groups were first allowed to watch the model dog producing food from the test apparatus 10 times by using her paw. After each of the 10 demonstrations the observer dogs were allowed to retrieve the food. After watching 10 demonstrations, the observer dogs were encouraged to manipulate the apparatus to get the food by themselves. Interestingly, while dogs in the control group and in the mouth-occupied group predominately used their mouth to manipulate the wooden rod, 83.33% of the dogs in the mouth-free group used their paw (Figure 7.2). We found the same significant differences when analysing the percentage of cases where the paw was used in
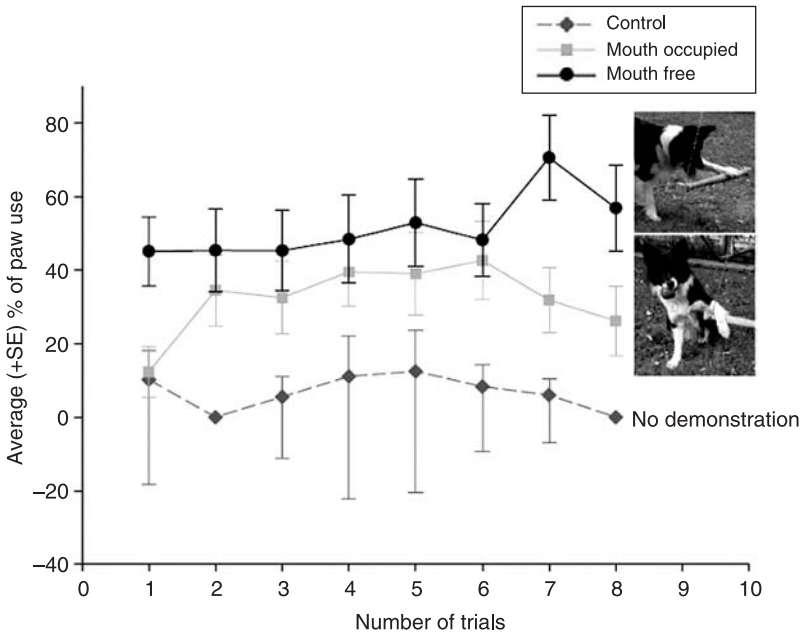
Figure 7.2 The mean percentage of paw actions of all manipulations in the two experimental groups and the control group over all trials (mean ± *SE*).

all manipulations, including unsuccessful attempts. Thus, the dogs' performance was comparable to that of the infants in the Gergely et al. (2002) study; they selectively imitated the model's action. Although all the dogs watched the same number of demonstrations, it is still possible that the selective reenactment resulted from a different level or focus of attention in the two experimental groups rather than from an inferential process, e.g., in the mouth-occupied group the presence of the ball may have attracted the observers' attention and thus led to a failure to notice the model's paw action. After the first trial, however, we continued testing the dogs in an additional seven trials, placing food in the container and letting the dogs operate the rod repeatedly. Significantly, by the second trial, the dogs in the mouth-occupied group also started using their paws, whereas the control dogs stuck to the mouth use. This later performance shows that the dogs in the mouth-occupied group learned the same information from the model as the dogs in the mouth-free group, but did not manifest it in their initial performance. Thus, attention alone cannot explain the differential performance of the dogs; other contributing decision-making processes must be assumed.

Directing the attention of others

In the previous sections it was suggested that social learning might strongly depend on how long the observer takes the opportunity to watch the model during a demonstration. In the case of animals the demonstrators are usually passive. Information transmission, however, would likely be much faster and more efficient if the knowledgeable model not only performs the behaviour to be learned, but also calls and thus directs the observers' attention to its actions and to the relevant aspects (Caro & Hauser, 1992). Nonetheless, in nonhuman animals only a few studies report active "teaching" behaviour on part of a demonstrator (Boesch, 1991; Thornton & McAuliffe, 2006). In contrast, in humans "teaching" communication seems to be the preferred way to interact with children. When showing something to others (educating humans or training animals) human demonstrators automatically check whether the observer is paying attention to their actions and if not, they stop the demonstration and try to reengage and then maintain the observer's attention. Even though animals as models typically do not actively call things to the attention of their observers, as observers they seem to be influenced by a human demonstrator's ostensive-communicative cues. In a study of human and nonhuman adult–infant communication during object manipulation, Bard and Vauclair (1984) showed that in contrast to human adults, adult apes rarely acted on the objects in order to direct or engage the infant's attention. Probably as a result, the infant apes were much more likely to attend to and manipulate objects when interacting with humans than with their own mothers.

   Compared to apes, domestic dogs may have evolved an even higher sensitivity to humans' attention-getting cues during the course of domestication.

When learning from humans, dogs seem to require the attention-getting, communicative behaviour of the demonstrator (Pongrácz et al., 2004). For example, seeing a human walking around a fence enhanced the dogs' detouring performance only if the human was talking to the observing dogs during the demonstration. Showing the solution without communication towards the dogs, did not help the dogs, even if the demonstrator had the reward in her hand. On the other hand, if the human model was talking to the dogs, seeing the reward was not necessary for successful learning. Thus, dependence on the communicative context is a further respect in which dogs' social learning is comparable to that of human infants. In the study of Gergely and Csibra (2005), where 14-month-old infants could observe an adult switch on a light-box by using her head instead of her hand, the children copied the novel head-action only if its demonstration had been accompanied by ostensive-communicative cues produced by the model. If these cues were absent, the children used their hand to press the light box, i.e., they did not copy the observed action.

Interestingly, dogs' learning performance does not depend on the same factors when they are learning from a conspecific. When a dog is demonstrating the detouring solution, ostensive-communicative cues like looking at the observer, calling the dog's name, or talking to the dog are obviously absent from the demonstrator's behaviour. Nevertheless, the demonstration is still effective (Pongrácz et al., 2004; Range et al., 2007). It seems that dogs' dependence on the model's communicative behaviour in social learning is specific to situations of learning from humans. This characteristic may be facilitated by the dogs' life-long experiences of humans targeting them and rewarding them for learning.

It is a further question whether the dependence of dogs' learning on humans' attention-directing behaviour reflects an understanding of the communicative meaning of these behaviours, e.g., eye contact, calling their name, dog-directed speech (Mitchell, 2004), hand-clapping, etc., or whether dogs react automatically to these cues. In order to answer this question, it would be interesting to repeat the detour task experiment with a human demonstrator who is talking to herself or who makes noise in some way.

CONCLUSIONS

Based on the results and arguments presented, we believe that domestic dogs should receive special attention in social learning studies. Given their unique evolutionary history and the way they are raised, their attentiveness and their ability to learn socially could originate from at least three sources. First, it is possible that dogs inherited high social attention from their common ancestor with wolves (Savolainen, Zhang, Luo, Lundeberg, & Leitner, 2002; Vilá et al., 1997). The common ancestor was probably a cooperatively hunting social species that exploited the behaviour of conspecifics. This evolutionary

origin would predict high social attention towards conspecific group mates. Second, since dogs typically grow up among humans, it is possible that their exposure to humans generalizes this social interest to their human companions. Third, the more than ten thousand years of domestication (Savolainen et al., 2002) may be an alternative source for developing an interest in human behaviour. According to these arguments, domestic dogs can be expected to be attentive towards and to learn socially from conspecifics as well as humans. However, after reviewing the relevant studies, it appears that different mechanisms may control these processes depending on the demonstrator species. Numerous results show that dogs are well prepared to pay attention to humans and to learn from them. These abilities partly reflect genetic changes that evolved during domestication and that are most probably further facilitated by the life-long learning processes of individual dogs. These make dogs a valuable species for comparisons with humans, since they may exhibit behaviours that are functionally analogous to human characteristics (Hare & Tomasello, 2005; Miklósi et al., 2004). Moreover, comparisons with dogs may at the same time have the effect of constraining hypotheses about the cognitive background of such behaviours.

Dogs may be especially interesting when the functions and the mechanisms of attention-directing processes are being investigated, since the domestic dog is the only nonhuman species that has evolved to interact with and to learn from members of the only species that practices teaching regularly, i.e., humans. That social learning in dogs may require the demonstrator to exhibit attention-directing behaviours might be influenced by the evolutionary processes assumed here, but this sensitivity appears only and specifically when learning from humans (Pongrácz et al., 2004).

In conclusion, we believe that the joint efforts of researchers studying social skills in humans, primates, and dogs will eventually allow us to disentangle convergent, divergent, and parallel evolutionary processes in the sociocognitive domain and will thus contribute to our understanding of the species-specific and shared abilities of cooperation and communication in humans.

8 From similarity to uniqueness

Method and theory in comparative psychology

Ingar Brinck

Comparative psychology is a strongly interdisciplinary field that shares many of its experimental methods and observational techniques with ethology and developmental psychology. The great variety of theories that comparative psychology evokes to explain behaviour generates a wide array of exciting and potentially fruitful accounts, but it is also problematic. It increases the risk of error in the forms of inconsistent background assumptions, conceptual misunderstandings, untestable hypotheses, and incoherent explanations, which in spite of being perhaps minor per se will impede scientific progress in the long run. Moreover, like psychology at large, comparative psychology tends to emphasize empirical investigations to the disadvantage of the analysis and development of theories and concepts. Consequently, disagreements stemming from areas other than methodology and experimental design do not receive sufficient attention. Furthermore, while evidence about biological evolution, i.e., the behaviour and cognition of ancient animals, is notoriously hard to find, the methodology for comparing the capacities of different species is under continuous development. This forces comparative psychology to rely on the adequacy of its theoretical and conceptual framework to a greater extent than is normally the case in the empirical sciences.

With an eye towards investigating the background of the problems facing contemporary comparative psychology, the present chapter examines central components of the methodology and explanatory framework of comparative psychology as well as its global objective.

FROM SIMILARITY TO UNIQUENESS

Comparative psychology investigates behaviour and cognition in human and nonhuman animal species mainly from a developmental and evolutionary perspective by contrasting observational and experimental data related to learning, control, and social interaction. It deals with interspecies similarity from two major perspectives, which correspond to Darwin's (1859/1936a) distinction between adaptive and nonadaptive similarities in terms of whether

an observed likeness provides evidence for related genealogy or not. An observed surface similarity in behaviour and physical appearance in two (or more) species that results from common ancestry constitutes a homology. Homology concerns the sharing of inherited, invariant traits and consequently the phylogeny or evolutionary history of species. If the similarity arises instead from convergent evolution in distant or unrelated species, it is a homoplasy, and originates from similarities in the respective external environments of the species. Knowledge of the ecological conditions contributes to determining the traits' selective pressures and whether they are universal effects of specific environmental constraints.

The comparative method is intended to expose behavioural differences between species that are ultimately relevant to determining what is special about human cognition. Using an experimental method, this can be done in one single step by directly focusing the investigation on finding significant differences. Thus, nonhuman animals are tested on tasks that tap typically human capacities such as theory of mind or imitative learning. If a sufficient number of subjects fail the test, a difference has been established. Of course, a mere difference in behaviour will be significant only if there is independent evidence that the behaviour actually is characteristic of the human species. For example, evidence might show the behaviour is indispensable for normal development in human infants, drawing on research in developmental psychology, or a prerequisite for human intelligence, say, human problem-solving capacities, falling back on cognitive psychology. An alternative approach employs a two-step procedure that does not call for initial support from research in other fields. The first step serves to reveal massive similarities in behaviour and perhaps in physiology and physical appearance and searches for ostensible differences that can be expected to indicate underlying cognitive differences. The second step takes these data as the starting point for framing hypotheses about specifically human types of cognition that can be tested in nonhuman animals.

"[T]hose who are fundamentally interested in evolution should be as delighted about similarities as they are about differences", asserts Hauser (1996, p. 68), claiming that it is as important to know how long and under what conditions a trait remained unchanged in evolution, as it is to know exactly what finally made it change. Hauser's remarks relate to the debate between the supporters of the phylogenetic approach to evolution and those who prefer an adaptationist approach. Towards the end of the twentieth century, the tradition of investigating phylogeny was heavily criticized from the point of view of adaptationism (e.g., Tooby & Cosmides, 1989). Whereas the former tradition focuses on the continuity of traits based in natural (gene) selection and tends to conceive of evolution as cumulative and stage-like, adaptationism examines discontinuity, or change in terms of the selective pressure of traits, picturing evolution as a process of dynamic specialization. Hauser refuses to side with either approach and contends that similarity and dissimilarity presuppose each other.

In fact, the concept of difference is a mere placeholder that indicates that something is missing, but not what should have been there, nor why it is absent. The significance of a typically human trait for the evolution of the human species cannot be understood unless its background in evolutionary history has been established. Then we are in a position to answer the question why the trait did not occur in other species. Consequently, though in principle important differences can be determined in one step (with some support from other areas of research), it is nevertheless vital to study interspecies similarities too. Once the relevant and fundamental similarities have been determined, informed and testable hypotheses are possible about the significance of any observed differences. For instance, knowledge about the overall similarity between two species and about the proximate causes of behaviour in the one species will permit inferences as to the kind of critical changes that once may have lead to the evolution of *Homo sapiens*.

Although comparative psychology does not explicitly accord human beings a special status, in practice, the human species frequently constitutes the core of the investigation, and nonhuman animals in general, disregarding species, form its contrast class. Much of the research rests on the largely implicit assumption that in the end any comparison between human and nonhuman animals will serve to throw light on the evolutionary history of *Homo*. This assumption has met with criticism and may provoke accusations of anthropomorphism. Nevertheless, it is quite modest and certainly does not presuppose that man is the measure of all things, but merely reflects a strong interest in human nature. For instance, Hauser (1996, p. 31) admits to a particular weakness for the search for human uniqueness, while nonetheless putting nonhuman animal species on an equal footing with the human species.

Those who prefer to think of human uniqueness as dependent on species-typical traits usually adopt a biological stance towards human abilities and are inclined to look at organisms as partially moulded by interaction with the environment. From a biological standpoint, any species is (equally) unique. In contrast, the view that there are species-specific human traits tends to covary with a developmental stance, which often entails focusing on capacities that unfold during human ontogeny. It suggests that uniqueness pertains to all of humanity; other animal species essentially are alike. With respect to the issue of human uniqueness, the biological and developmental stances roughly organize comparative psychology into two contrastive fields. However, the fact that they put a broad emphasis on human abilities makes them both anthropocentric. A moderate anthropocentrism does not threaten scientific objectivity, but simply expresses the perspective of the first-person plural ("we"), a collective point of view. As Karin D'Arcy (2005, p. 182) observes, anthropocentrism and the phylogenetic approach (which incidentally considers natural history from a third-person perspective) are equally valid in comparative psychology.

Of course, the central position of human behaviour and cognition in comparative research will influence the general method. For instance, a preference

for animals that share the evolutionary history of the human species and whose study can be expected to illuminate human psychology guides the selection of species that are investigated. In contrast, animals that show relevant behavioural similarities to human beings, but do not share a significant part of their gene pool, receive less attention.

CULTURE, LEARNING, AND THE NATURE OF HUMAN UNIQUENESS

The issue of human uniqueness lies at the heart of comparative psychology. This makes clarifying the nature of the uniqueness a central concern. Expressions such as "human uniqueness" and "critical difference" seem to suggest that a single ability, say, for recursive grammar (Hauser, Chomsky, & Fitch, 2002) or imitative learning (Tomasello, Kruger, & Ratner, 1993), is responsible for the evolution of the human species. This ability may involve more than one variable. In favour of the latter view, Matsuzawa (2007) argues that humans and chimpanzees share the intrinsic motivation to copy other individuals' actions, although only humans can learn from a single trial ("generalized imitation") and engage in overt teaching. Yet, even if the existence of an adaptation that indicates the birth of humankind had been conclusively established, it could not justify the conclusion that there exist particular traits specific to or original with *Homo sapiens*. The difference between *Homo* and its closest ancestor may equally well be a matter of degree as one of kind. Thus, Darwin asserted, "the difference in mind between man and the higher animals great as it is, certainly is one of degree and not of kind" (1871/1936b, p. 494). Along these lines, Langer (1998) maintains that primate skills are essentially the same, taking causal knowledge as an example. He holds that heterochronic structural changes have caused causal skills to develop more in humans than in other primates, because cognitive mechanisms that previously developed consecutively have been reorganized and now develop simultaneously, in alignment. This would permit these capacities to interact while they develop, pushing them in the direction of higher complexity. Then again, uniqueness may have derived from existing abilities, by either a gradual, continuous change or a radical shift in them. Gradual change can be purely quantitative and occur once a critical level of organizational complexity is reached (Greenberg, Partridge, Weiss, & Pisula, 2004). Accordingly, Hatano and Takahashi (2005) conjecture that there is only a small difference in many basic abilities between humans and great apes, but that the aggregate of a number of them produces remarkable qualitative differences in collaborative skills, culture, and cognition.

Each of the enumerated hypotheses is plausible in its own right. The available evidence in the field is not strong enough to underwrite a decision for or against any of them, and at this point, none of them can be dismissed on purely empirical grounds. In these circumstances, approaching the issue of

human uniqueness by discussing the manifest capacities it supports rather than what might have brought it about in evolution will prove more revealing.

In the eyes of many, the capacities for symbolic knowledge, culture, and art make human beings special. Humans are exceptional teachers and learners, who pass on knowledge between generations while changing and augmenting the insights of previous generations. This permits knowledge to grow and technical skills and technology to increase over time (cf. "the ratchet effect"; Tomasello, 1999). During the last few decades, research on human uniqueness has centred on the enabling role of imitation and cultural learning for these capacities (Tomasello & Rakoczy, 2003). According to Tomasello and Call (1997), imitation means that the observer attempts to reproduce selectively the means and ends of another agent's action while paying attention to its goal-directedness. This makes it possible to understand both the details and the global systematic properties of an action.

Describing culture as behaviour that is specific to members of a group and is socially transmitted, Caldwell and Whiten (2002, 2006) consider the difficulty of identifying a criterion of demarcation between cultural and implicit learning. Contrary to cultural learning, implicit learning does not require the supervised attention of either teacher or apprentice. Genetic and environmental factors sustain it, as does taking part in common, daily activities and sharing routines. Caldwell and Whiten draw attention to the numerous approaches to cultural learning in the field, which use different methodologies and conceptual frameworks and thereby make comparison of theories and experimental data virtually impossible.

The aim of establishing whether any other primate species has at least rudimentary cognitive capacities for typically human behaviour and perhaps could have evolved a variety of it under different evolutionary circumstances motivates the search for a criterion of demarcation. However, the multifaceted nature of human learning strategies makes it likely that looking for a sharp boundary between distinct forms of learning is misguided unless the purpose is purely analytical. Different forms of learning do not seem to operate independently. Although they characteristically control different types of behaviour, they still interact, performing complementary roles. Furthermore, the intentional forms of learning that emerged later in evolution seem less self-sufficient than those that evolved at earlier stages. For instance, humans perform better on a pragmatic level of action that engages the agent on a personal level but does not extend much further than the present context than on one that requires abstraction and conceptual reinterpretation (Gallagher & Marcel, 1999). The meaningfulness of pragmatic action typically depends on emotional engagement and socially constituted properties of the surrounding context. Given the heavy costs of (at least) time and mental effort attached to imitation and cultural learning, and taking into account the indirect nature of the benefits, one might expect these forms of learning to exploit simpler and cheaper heuristics routinely, as other complex cognitive capacities do. In order to function adequately in daily life cultural learning,

clearly not an exception in human behaviour, would seem compelled to rely on other, preexisting ways of gaining knowledge, which support social and physical action in primates generally.

Emulation, social facilitation, and stimulus enhancement all exploit contextual affordances. These forms of learning automatically aim for efficiency and not for replication or perfection of the other agents' actions—contrary to cultural learning, which aims to maximize performance. In comparison, imitation and cultural learning are time consuming and costly in terms of resources. Given a biological outlook, it makes sense to think that at least some of the capacities that typically bolster human behaviour also occur in other primate species and have a similar basis.

Hence, human uniqueness seems to depend on a network of abilities, practical and decontextualized, implicit and explicit, that integrate typically human capacities with those possessed by other animals, especially other primates. The capacity for flexible integration of them may be as important as the capacity for imitation and cultural learning. Although imitation and cultural learning certainly seem to be prerequisites for human uniqueness, they do not explain it and in all likelihood cannot produce it on their own. Behind the strong focus on a species-specific learning mechanism lurks a view of human uniqueness as virtually cut loose from the circumstances that produced it. In minimizing the contextual contribution to cognition, this view prevents an understanding of the broad, environmental impact on the mind and it plays a minor role in contexts of explanation that emphasize ecological conditions.

An evolutionary, ecologically minded outlook on cognition has more in common with the approach in philosophy and cognitive science that describes the mind as embodied and extended (Clark, 1997; Clark & Chalmers, 1998; Varela, Thompson, & Rosch, 1991). Cognition is a situated practice, based in active perception and controlled by local and physical as well as global and sociocultural contextual features. Internalized skills interact with suitable properties of the environment to produce specific actions, and, in turn, emerging forms of behaviour induce changes among existing environmental conditions. The dynamic between agent and environment shapes cognitive processes in real time.

Biological evolution and in a shorter historical perspective sociocultural construction have tuned relevant aspects of the environment to the needs and abilities of human beings. Much like other animal species, humans take advantage of the environment to offload cognition for future purposes and reconstruct it to enhance the manner in which it supports their activities. The environment reciprocally structures human behaviour by providing long-term scaffolding for recurring activities. Theoretical knowledge, skill, and techniques all are embodied and materialized in tools and artifacts as well as in shared behaviour patterns like conventions and habits. Since the physical and functional properties of the means influence the nature and content of action, factors such as technical and manual know-how, economical resources, methods for representing knowledge, and access to significant raw

materials control a social group's level of cognitive complexity. The elaborate and escalating division of labour between organism and environment might explain the success of the human species in transmitting and increasing shared knowledge.

Thus, human uniqueness seems to depend on a variety of typically, in some cases perhaps specifically human forms of behaviour. They can be summarized in a few, general capacities. Whether *Homo* shares them with other primates and, if so, to what extent, has not been settled yet. Thus, humans externalize their ideas in socially shared, technical tools that afford control and sometimes even symbolic and abstract representation, e.g., pictures and mathematical notation (cf. Vygotsky, 1978). Using pieces of rock to make tools and symbols to model and develop tools provide two examples of how humans can engage in higher order tool use and explicit metacognition by employing technical tools to manage manual ones (Kirsh, 2005). Additionally, psychological tools help to control the self relative to the physical and social environments. In recruiting the physical context, these tools improve performance and let the agent regulate his or her actions and skills, as in the act of putting coins in even piles when counting them to keep track of the amount (Kirsh, 1995). Finally, the struggle to improve what is already working, and not stop at satisficing as other animals apparently do (Simon, 1955), is probably both a universal and decisive feature of human behaviour.

USING MORGAN'S CANON

The term "comparative psychology" originally concerned the study of intelligence, operationalized in terms of the capacity for learning (Romanes, 1883). This approach set the agenda for future research by granting learning a prominent position in the field. Following Romanes, comparative psychology in its initial phase relied on informal observations and anecdotal evidence while deriving the explanations of behaviour from generalizations based on introspection. Today the impossibility of corroborating anecdotal evidence is widely recognized and like introspection, it is rarely used.

Lloyd Morgan brought about a change in the direction of a more rigorous methodology. Morgan (1903) disapproved of attributing higher order mental processes that normally are associated with human intentional actions to animals, arguing that these processes must first be analysed into the simpler ones on which they depend. The rationale behind this modus operandi— known as Morgan's Canon—is twofold. First, unless independent evidence can be obtained for the higher level processes in the animal, its behaviour should be interpreted in terms of more probable, lower level processes. Second, given that an explanation of an animal's behaviour on a lower level is adequate, it may be used to shed light on related behaviour in human beings. If successful, such a reinterpretation of human behaviour will show that a simple but general mechanism has been mistaken for a specialized one.

The relations between the different processing levels of behaviour still constitute a central issue in comparative research. Morgan's Canon incites controversy, and its proper interpretation is a matter of dispute (Allen-Hermanson, 2005; Karin-D'Arcy, 2005; Montminy, 2005). The principle is frequently taken to downgrade the capacities of animals, not only because it endorses describing animal behaviour in nonintentional terms, but also because the term "lower level processes" implies processes that are less "advanced" than the so-called higher level ones in human beings. A principled denial of higher level processes in animals presupposes a rather crude difference in kind between human and nonhuman animals for which we have no evidence at present. Moreover, the default position of describing only typically human behaviour on higher levels excludes certain interspecies comparisons by definition and, in addition to being arbitrary, it is counter-productive in comparative psychology.

Even so, this is not a reason to reject Morgan's Canon. Putting aside Morgan's speculations about the evolutionary process, we can take Morgan's Canon as telling against *any* explanation of behaviour in terms of higher order abilities, unless, in Morgan's words, "we already have independent evidence of the occurrence of these higher processes in the animal under observation" (1903, p. 59). This procedure seems plausible whenever a behaviour "can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (p. 59)—regardless of whether the behaviour is found in human or nonhuman animals.

On this interpretation, Morgan's Canon is a reasonable but cautious methodological principle. It does not have much in common with the principles of parsimony, simplicity, and efficiency, nor with reasoning by analogy in spite of the many efforts to account for it along both of these lines. It recognizes that until there is evidence to the contrary, any behaviour should be described on a neutral level that does not a priori exclude human processes in other animals—given that a neutral description is both possible and rational relative to available evidence about the behaviour in question. Morgan's Canon appeals to reason and takes the situation at hand to be informative enough to permit a knowledgeable decision about the interpretation of behaviour.

It is sometimes argued that Morgan's Canon has lost its importance. This position is surprising given that even today human and nonhuman behaviour that appears identical with respect to morphology and function is regularly operationalized differently—even in the absence of independent evidence or adequate reasons that would support the practice. The approach is especially troublesome with regard to the closest (living) ancestors of the human species, the great apes, as it runs the risk of concealing significant similarities between the species.

The research on intentional, nonverbal communication tends to describe the behaviour of human infants in terms similar to that of adults. Yet, there is at present no evidence that the processes that support nonverbal

communication in infants are similar to those that supposedly are operative in adult verbal communication, e.g., higher order (metacognitive) judgements or desires about the desires and beliefs in oneself or other speakers. Consequently, while great care is taken to avoid intentional terms in describing the communicative behaviour of the great apes, the opposite approach prevails concerning human infants. Whether this practice might be independently justified is so far unclear. Recent attempts to show that the mind of human infants is radically different from that of the great apes have not met with much success. Yet on a deeper level of analysis there are unmistakable differences related to social interaction (Bard, 2005; Matsuzawa, 2006; Tomonaga et al., 2004).

The tendency to account for observations of similar behaviour in human and nonhuman animals on different levels of explanation seems deeply ingrained in human nature. In contrast, the reading of Morgan's Canon presented here encourages describing the behaviour of nonhuman and human animals on a nonintentional level, as long as evidence to the contrary is lacking. This strategy at least allows for making unbiased interspecies comparisons.

Although contemporary research on nonhuman primates may still find methodological behaviourism attractive, developmental psychology considers it obsolete. That these opinions differ does not present a problem as long as the two fields are kept apart. However, in the field of comparative psychology similar methodological principles must apply to all species considered. To think otherwise is to renounce the fundamental tenets of the discipline. Letting distinct methodologies guide behavioural studies in nonhuman and human animals without a proper justification would make comparative studies pointless. For instance, suppose that different methods were regularly used to describe the performance of human infants and apes during the same kind of experimental conditions, and that human behaviour was consistently analysed on more complex levels than that of apes. This would bias the outcome of the experiments in favour of the humans and consequently would not be acceptable.

COSTS AND BENEFITS OF TINBERGEN'S EXPLANATORY MODEL

Partly because of Morgan's criticism, comparative psychology adopted a behaviourist methodology and focused on learning mainly in rats, pigeons, and dogs in an effort to reveal the simple processes that control complex behaviour. The approach was thoroughly mechanistic. Eventually research in ethology made comparative psychology regain interest in the evolutionary approach to behaviour, and the range of experimental techniques increased as did the number of species to which they were applied.

In 1963, Niko Tinbergen presented an explanatory model that still exerts a

major influence on comparative psychology. Tinbergen's model (henceforth TM) brings together several questions about the causal origin of behaviour in a single model. By systematically relating four different types of cause, Tinbergen managed to develop a unified methodology for the study of animal behaviour. In addition to offering a model for the explanation of behavioural data, TM provides tools for generating and analysing hypotheses about the relations between the causes and particular behaviours. Thus, TM has a double function: It is both explanatory and exploratory.

Tinbergen held that a comprehensive explanation of a given behaviour requires establishing the following causes:

1   The (neuro)physiological mechanism that produces and controls it in real time.
2   Its ontogeny (or development).
3   Its adaptive significance (or adaptive function).
4   Its phylogeny (or evolutionary history).

The first and second causes occur during the lifespan of an animal, and the last two belong to the evolutionary history of its species. The third cause, adaptive function, concerns natural selection in terms of heritable variation or genotype and explains why a species has evolved a given behaviour. The fourth cause, phylogeny, traces the history of the behaviour within the lineage of one or more species.

It is important to conceive of all four causes as historical. The nature of adaptation is especially likely to be misunderstood, often characterized as "forward-looking", or worse, said to involve backwards causation. The latter readings of the concept of adaptation mistake the very process of adaptation, which is an outcome of natural selection, for a teleological one that would make the final state of the adaptation causally efficient in its production. Mayr (1974) provides a concise refutation of this construal, arguing that natural selection is strictly an a posteriori process; even though it rewards current success, it never sets up future goals. By acting on behavioural output, natural selection can reward past events that have produced successful recombinations of genes. Accordingly, there is no reason to refer to the future benefit of behaviour in terms of its survival value or fitness to explain how traits perpetuate themselves from generation to generation.

Furthermore, Mayr (1974) makes it clear that detachment is necessary for the flexibility that characterizes natural selection, and permits the organism to adjust to changes in the environment. Had evolution been teleological, it would have been predetermined and could not involve flexible adaptation in the present sense. Consequently, the very idea of biological evolution excludes both that adaptation might be governed by future benefits and that evolution might be a process that gains in efficiency or proceeds towards more complex levels.

Tinbergen emphasized that although a complete explanation will invoke all

four causes, initially each cause should be examined separately. The underlying rationale is that the causes concern mutually independent areas of investigation. Investigating them together, using the same conceptual framework, does not permit one to distinguish between the roles that the different causes play in the behaviour under investigation, and consequently will not result in an adequate explanation. The following description of how causes relate to concepts may clarify the point.

Causes in themselves do not explain anything; rather, a particular cause acquires an explanatory function when it is conceptualized in terms of an aspect of a cause within a given conceptual structure. The significance of a given cause derives from the theory that articulates the conceptual structure and puts flesh on the bones of the structure. For example, consider the different ways in which various accounts of biological evolution reconstruct events by emphasizing continuities or discontinuities, processes or events, dynamic or static properties, etc. Different theories tell different stories.

Inductive generalizations and general hypotheses about specific mechanisms concern the testable aspects of causes of a certain theory. In systematically relating empirical data, hypotheses, and generalizations, the theories not only explain, but also enable exploratory work by providing precise tools for making predictions and generating hypotheses.

Viewed from an empirical perspective, the four causes in TM are, of course, related. The fact that the concepts of the causes are embedded in logically distinct conceptual structures makes it possible to approach them individually and then use them to illuminate each other. In an individual context of explanation, the four causes will relate to each other in precise ways, e.g., the particular developmental path of an organism depends on both its physiology and the evolutionary history of the species to which it belongs, yet as a matter of fact the same ontogeny might have had another sort of phylogeny and resulted from another adaptation.

Tinbergen stressed the importance of working towards comprehensive explanations of behaviour, of attempting to integrate the individual explanations once established. This enables them to completely cover the problem space and form a coherent whole by not leaving any gaps in the account. Though based in different conceptual domains, they should tie into each other conceptually at some points. Basically, there are two reasons to argue for an integrated approach to behavioural studies, which relate to the explanatory and exploratory functions of TM.

Regarding the explanatory function, Ryan (2005, p. 436) argues that "employing the four aims and methods of Tinbergen in isolation is not sufficient, but these aims and methods need to be integrated to have an understanding of the biology of behaviour that is both [empirically] correct and complete". Autumn, Ryan, and Wake (2002, p. 405) point out that even if a researcher is only interested in one cause, attending to all four is "necessary to reach a robust and rigorous answer". The rationale of the claims comes from the fact that, empirically speaking, all four causes connect. This is why

comparing the individual explanations can reveal errors in them. Hence, researchers cannot be sure that their explanations are correct unless they have checked for possible interference from the other causes.

As to the exploratory function, TM is a tool for generating and testing hypotheses about adaptation and phylogeny. The difficulty of finding hard evidence for evolution makes analytical tools for generating testable hypotheses more important in comparative psychology than in most empirical sciences. The value of TM in this area presupposes that the different causes and conceptual structures are carefully distinguished. A coherent and consistent integration of independent explanations will result in a synergy effect, because questions in one domain then can suggest evidence for questions in another domain (Ryan, 2005). For instance, knowledge of adaptive function can provide clues to the cognitive mechanisms of a species. Thus, having established the ecological conditions that give rise to food caching in a certain species makes it possible to frame testable hypotheses regarding the animal's capacity for spatial memory (Autumn et al., 2002).

Tinbergen acknowledged that studying phylogeny enables one to understand whether a similarity in function is a homology or homoplasy. Since similar selection pressures can give rise to similar traits in two species regardless of whether they share the ancestors or not, the degree of divergence from a common ancestor can be determined by phylogenetic tools. Analogous tools are used to test hypotheses about adaptation that make predictions about the associations of traits within species by, say, size and mating system. An example concerning the evolution of language illustrates the benefit of this approach (Weiss & Newport, 2006). Suppose that primates exhibit capacities similar to human infants in speech perception or in language processing. Then it is reasonable to assume that these capacities are homologous. We can conclude that they did not evolve specifically for language acquisition and rule them out of the account. To summarize, examining separate explanations in the light of each other permits one to extract information that is not available upon individual inspection This means that integration increases the predictive and explanatory power.

However, integrating the explanations requires more than simple alignment and sometimes proves quite hard. Bolhuis and Macphail (2001) argue that disagreements about seemingly substantial or concrete issues often have their origin in a misunderstanding about the significance of the four causes. Their claim points in two directions. Confusion about the various roles of the causes of behaviour amounts to a conceptual misunderstanding that springs from insufficient theoretical knowledge. Conversely, procedural mistakes constitute methodological misunderstandings that stem from a failure to investigate the causes separately.

The error of using concepts that belong to different structures in the explanation of a single cause arises from a misunderstanding of the concepts' meaning. Since the explanation derives from theories that articulate distinct conceptual structures, it will misrepresent the cause. In concealing the actual

state of affairs and the fact that there is more to know, the error constitutes an epistemic risk (Sahlin & Persson, 1994): Ignorance, or not knowing, leads to the same mistakes as erroneous knowledge. The effects of this error on comprehensive explanations are serious. This error prevents the updating of information about one of the causes without overthrowing the entire explanation, and it obscures the relations between the causes, information about which is vital for the exploratory use of TM. The error of approaching all four causes in one fell swoop issues instead from a methodological misunderstanding. In directly proceeding to give an integrated account, the inquiry will fail to ground the causes in their respective conceptual domains. Consequently, the exploratory function of TM will be lost.

An improperly analysed conceptual system is unreliable and provokes arbitrary definitions and tautological (or circular) hypotheses. In an analysis of five studies in developmental psychology, Smedslund (1994) elucidates the kind of errors that result from inadequate and insufficient conceptual analysis and cause experiments to misfire, e.g., hypotheses that rely on implicit theoretical assumptions or assumptions about capacities that have not been independently established. Smedslund's conclusion deserves attention, for it is of immense importance to comparative psychology and empirical research in general: *A hypothesis is empirical only if the variables it contains are semantically and logically independent*. Violating this rule makes it impossible to use TM for any purpose. Explanations that do not distinguish between the conceptual domains of the causes will not be able to profit from Tinbergen's approach.

THE PRACTICE OF EXPLAINING BEHAVIOUR: SOME FUNDAMENTAL PROBLEMS

Reconstructing the evolution of human cognition is challenging, not only because it requires integrating knowledge from areas that approach the topic in very different ways and do not cooperate as a rule. In addition, evidence about the life and behaviour of ancient animals is scarce and difficult to come by. The paucity of evidence encourages an interest in alternative sources of information, e.g., studies of the fossil record. It also causes comparative psychology to expand into new fields. Developmental psychologists, ethologists, and primatologists now work together with neurophysiologists, geneticians, archaeologists, philosophers, social scientists, and palaeontologists. The first group conducts the major part of the work and agrees on a few fundamental, mainly methodological starting-points for the research like the relevance of various kinds of data, how to operationalize observations of behaviour, and which experimental methods to employ. They also share a general explanatory framework.

Then again, this framework is sketchy and complicated at the same time. It is sketchy, because following TM it boils down to asking for an explanation

of the four causes of behaviour and might as well be described as part of methodology. Accordingly, it stands in need of interpretation to elaborate its structure and content and to permit the fine-grained categorizations of the aspects of the causes, the various relations among the causes, and the relations between the causes and the environment to be determined. The explanatory framework also is complicated, because it has several independent, sometimes inconsistent interpretations, and it does not impose any specific constraint on the ways in which they may connect.

In view of these two points, one might say that the explanatory framework of comparative psychology provides a playing field, rather than restraining ongoing activity. Despite the existence of a shared methodological foundation for the research, disagreement stemming from opposing views on fundamental issues is not unusual. Unfortunately, the sources of these disagreements are not regularly made explicit, perhaps because no common conceptual framework has yet materialized within which to discuss them. This particular problem has its source in the continuous reinterpretation of the original theory of evolution.

Ever since the inception of the field of natural history, rival accounts have attempted to spell out the details of Darwin's theory. New approaches are advanced that agree in the main, while they are tailored to the specific purposes of particular subfields in biology. The explanatory framework of comparative psychology incorporates the more successful ones, each one offering a way of making sense of adaptive change and evolutionary history with precise effects on the use and outcome of the explanatory model. No one account has won out; they continue to exist side by side. As a result, an explanation of behaviour may refer equally to concepts and principles that had currency at Darwin's time and to others that have been introduced more recently. Although most approaches share the central concepts of the theory of evolution, it cannot be taken for granted that they interpret them in the same way. This leads to considerable leeway in applying the theory of evolution to explanations of behaviour and produces misunderstandings and disagreements. Hence, it may be quite difficult to disentangle the variety of positions taken towards a given phenomenon, the more so since the theoretical assumptions and methodological principles of individual accounts are rarely made explicit.

Rakover (1990) discusses an imbalance between explanatory model and theory similar to the one discussed previously. He claims that applying several explanatory models to the same behavioural domain leads to an inundation of ad hoc theories. This has the consequence that if a given phenomenon cannot be accounted for by one model, it will be replaced by another one, until a model is found that works. This means that theories are merely abandoned instead of falsified. Rakover's scenario illuminates certain aspects of contemporary comparative psychology, where a growing number of interpretations of evolution are clustered around a single explanatory model. Rakover also discusses the case where several theories compete over a single

explanatory model. He points out that this imbalance fosters confusion between competition among models and competition among theories. Such confusion can be found in comparative psychology, too.

The many interpretations of biological evolution not only affect the content and inferential patterns of theory and concepts, but also increase the importance of rules of thumb and pragmatic principles in evolutionary studies of behaviour. Comparative research sometimes seems to make generous use of heuristics, e.g., to bridge theories that articulate different conceptual structures and in order to compensate for the lack of raw data. Accordingly, idiosyncratic, contextual maxims may have a significant impact on the research and may indirectly influence the development of theories and concepts. These relevant maxims can be grouped systematically according to their respective functions in explanations of behaviour. First, prescriptive principles, e.g., Morgan's Canon and Tinbergen's explanatory model, provide support in methodological issues and mainly concern procedure. Second, retrodictive principles, e.g., inference to the best explanation and the principle of parsimony, have a pragmatic function and express paradigmatic behaviour. They provide guidance when a knowledgeable decision is not possible. Finally, predictive principles, e.g., the comparison of independent causes and analytic and phylogenetic tools, are heuristic and support data collection, hypothesis framing, and generation of tests.

In analysing the contemporary state of research in psychology, Machado, Lourenço, and Silva (2000) declare that the progress of psychology at large relies on balancing investigations in the areas of theory development, conceptual analysis, and experimental research, which are all equally important. In line with this view and using their framework, one might claim that contemporary comparative research tends to emphasize factual investigation to the disadvantage of the other two areas. This bias has introduced a gap between methodological issues on the one hand, and theoretical and conceptual issues on the other. The gap will grow as long as scientific progress is driven by experimental research and pursued from the bottom up; moreover, it threatens to make theory immaterial to empirical work. As Machado and colleagues observe, due to the imbalance among the resources that are invested in the three areas, the research on theoretical issues and their conceptual foundation is underdeveloped in comparison to methodological questions. Thus, general and important claims can be found in the literature that are not systematically backed up by adequate evidence as well as experimental work that yields conclusions that are neither explicitly related to a particular theory nor derived from properly justified generalizations. Nevertheless, in the field of comparative psychology there is a growing awareness of the kind of difficulties that this chapter has pointed out. However, the discussion of theoretical and conceptual issues from a general perspective needs to be intensified in order to overcome them. The present chapter attempts to spell out and systematize some of these problems with the aim of promoting this discussion.

ACKNOWLEDGEMENTS

Part III

Culture

9   Experimental approaches to the study of culture in primates

Christine A. Caldwell

The topic of culture in nonhumans has received a lot of attention in recent years, and perhaps this is not surprising. The idea that other animals—apes, monkeys, and maybe even rats and fish—may show a semblance of a trait that we consider to be so fundamentally human, is both exciting and controversial. Dialogue between enthusiastic advocates of animal culture on the one hand, and wary sceptics on the other, has therefore generated a fruitful intellectual atmosphere, and spawned a broad, rich, scientific literature on the topic.

In this chapter I hope to illustrate how this atmosphere has been particularly influential in generating innovative and informative experimental approaches to the study of culture, due to the need for controlled (and hence less ambiguous) observations. The consequence of this has been that the experimental literature on culture in nonhumans now has much to offer research on human culture, and exposes gaps in our current knowledge within this area. Although there is a literature on experimental approaches to human culture, it is far from extensive, and studies are somewhat scattered. I will therefore also review some of the experimental research that has been carried out on human culture, drawing comparisons with the animal research.

This chapter will focus specifically on the topic of primate culture in discussing the nonhuman research. There are two main reasons for this narrowing of focus. The first of these is that experimental research on primate culture has necessitated a somewhat more ingenious and creative approach than research on other animals, such as fish and rats (this is an issue that will be returned to later), as practical and ethical issues restrict what can be done. Since these constraints certainly apply to work with humans as well, then it is likely that these approaches might prove to be particularly useful in researching human culture. The second reason for the primate bias in this chapter is simply that, as our closest evolutionary relatives, primates can reasonably be expected to share with humans a greater number of attributes than any other phyletic group. Therefore, whatever form "culture" takes in these species, it is liable to show more similarities with human culture than other animals' behaviour would. Again, this serves to increase the chances that we may be

able to usefully extrapolate some of what we have learned from animals, to enhance our understanding of humans.

OBSERVATIONAL APPROACHES TO THE STUDY OF CULTURE IN NONHUMAN PRIMATES

Those who study animals typically define "culture" as behaviour that is specific to a group, which is transmitted via some form of social learning (see Caldwell & Whiten, 2006, for more detailed discussion). Observational approaches to studying culture in primates have therefore focused first on identifying group-specific behaviours. In order to be cultural though, any between-group variation, or within-group similarity, must have arisen as a result of social learning. So researchers must also attempt to rule out competing explanations, such as genetic differences between the groups, or different environmental conditions.

Such observational approaches have provided abundant data on behavioural traditions in primates. Researchers have been able to compare data from different field sites in order to show striking variation between groups. One of the first systematic studies of this type was carried out by Whiten et al. (1999). Data from the seven longest-running chimpanzee field sites was pooled in order to determine whether there were differences in behaviour across sites. Research directors from each of the study sites were presented with a list of 65 behaviours, each of which was suspected to show variation across sites. The research directors reported which of these behaviours they had observed in their study population, and with what frequency. Of the original list of behaviours, a total of 39 were identified as being either customary (the behaviour occurred in all or most individuals of at least one age-sex class) or habitual (the behaviour occurred repeatedly in several individuals) at one or more of the sites, whilst being absent from at least one other, with no apparent ecological reason for the absence. Whiten et al. concluded that these behaviours were therefore likely to be culturally transmitted. The list included a range of activities, including tool-use behaviours (such as termite fishing and nut cracking), social gestures (such as the grooming "hand-clasp"), and behaviours with a hygienic function (such as the "leaf-napkin").

Since the publication of Whiten et al.'s (1999) article, similar surveys have been carried out for other primate species, with similar findings. Van Schaik et al. (2003) surveyed orangutan field sites, also identifying a list of behaviours that were customary or habitual at certain sites, whilst being absent from others. Striking behavioural variation between groups of white-faced capuchin monkeys has also now been identified, in both their social behaviours (Perry et al., 2003) and foraging behaviours (Panger et al., 2002).

However, there are limits to what can be learned from purely observational data. Some authors have argued, for instance, that it is simply not possible to

claim that group-specific behaviours are cultural, due to the fact that there is always a certain amount of doubt about whether they have been socially transmitted (Galef, 2003; Laland & Hoppitt, 2003). Researchers can do their best to rule out the likely competing explanations, but these can never be completely eliminated as possibilities. Galef (2003) in particular has argued that the group-specific behaviours observed in chimpanzees are likely to be the result of differential reinforcement contingencies, arising as a result of different environmental conditions. In other words, the variation in behaviour is purely attributable to individual trial-and-error learning, made possible by different surroundings (see also Galef, 1995). This is a difficult point to defend against, since there are always likely to be subtle differences between environments, which may not be immediately obvious as sources of variation in behaviour, but which could nonetheless have such an effect. Galef (2004) and Laland and Janik (2006) have drawn attention to the two contrasting methods of "ant-dipping" behaviour observed at different chimpanzee field sites: Chimpanzees from the Tai forest use a simple technique involving a short stick; those from Gombe use a more complex bimanual technique employing a longer stick. However, chimpanzees from Bossou alternate between the two, depending on the species of ant (Humle & Matsuzawa, 2002). Galef asserted that such a finding is not consistent with a hypothesis of traditional behaviour, and Laland and Janik have suggested that the Tai and Gombe variants may well have been shaped by the local conditions at each site.

Over recent years, field research on culture in primates has utilized increasingly more sophisticated methods, which make it less and less likely that explanations other than social transmission could account for the patterns of behaviour observed. Caldwell and Whiten (2006) have discussed how approaches that either focus specifically on social behaviours, or those that use social contact as a variable in analyses (Panger et al., 2002; van Schaik et al., 2003) are extremely difficult to refute as examples of cultural behaviours. However, in order to directly test hypotheses about whether the behaviour of other individuals affects the likelihood of adopting a behaviour oneself, experimental manipulations are necessary.

Laland and Hoppitt (2003) have argued that to date the best evidence of cultural behaviour in nonhumans comes from fish. Laland and Hoppitt cite Helfman and Schultz's (1984) work on reef fish, *Haemulon flavolineatum*. Helfman and Schultz were able to carry out a direct manipulation of the fishes' social environment, independent of their physical environment. They introduced a fish population to an area where another population already existed, finding that the introduced fish subsequently showed the same preferences for schooling sites and migration routes as the preexisting members of the population. However, a further naïve population were later introduced to the same site, but this time, all other fish had been removed from this site. What they found this time was that the fish developed entirely novel preferences for schooling sites and migration routes. This direct manipulation of

the presence or absence of experienced individuals had the power to demonstrate that the social environment was far more influential than the physical environment in determining the preferences of newcomers.

However, as Laland and Hoppitt (2003) acknowledge, such manipulations would be unfeasible with primates, for a variety of reasons. Moving large numbers of primates from their natural environment for the purposes of carrying out an experiment into social learning would be not be ethical, as well as being likely to be logistically a lot more complicated than moving populations of fish.

EXPERIMENTAL APPROACHES TO THE STUDY OF CULTURE IN NONHUMAN PRIMATES

Nonetheless, experiments in which the social experiences of primates are actively manipulated have become commonplace within the literature on social learning, although these have not taken the form of translocation experiments, such as that carried out by Helfman and Schultz (1984). Researchers have instead been able to carry out experiments with captive primates, in zoos and laboratories, in order to investigate the effects of observing the actions of experienced conspecifics. To a limited extent, field experiments have also been possible with wild primate populations (see Galef, 2004, in which such an approach is strongly advocated). This section will review the various approaches to investigating culture in nonhuman primates experimentally.

Dyadic experimental designs

In dyadic experimental designs, a naïve observer animal is exposed to another, experienced, individual performing a particular behaviour. The earliest examples of such experiments involved a simple comparison between an experimental condition (in which subjects are exposed to a demonstration), and a baseline condition (in which no such experience is provided). Studies using such a design typically find that subjects that have been exposed to the demonstration are subsequently more likely to perform the behaviour themselves, or do so more quickly, than those in the control group. Warden and Jackson (1935) and Tomasello, Davis-Dasilva, and Bard (1987) carried out experiments of this type, with rhesus macaques and chimpanzees, respectively.

These experiments certainly show that the behaviour of other individuals can affect the likelihood of that behaviour being adopted by a naïve individual. However, a more powerful experimental design involves contrasting the effects of different demonstrations. If social learning mechanisms have the power to sustain divergent cultures in separate social groups, we would expect that alternative versions of a demonstration would generate contrasting behaviours in different experimental groups.

Primatology has therefore made good use of a methodology developed initially to test for imitation in budgerigars (Dawson & Foss, 1965). Dawson and Foss devised a "two-action" method. Two-action designs involve two alternative demonstrations on the same object, with each producing the same end result. In Dawson and Foss's study, naïve budgerigars observed a trained conspecific accessing a hidden food reward by removing a lid with either their beak or their feet. Dawson and Foss then recorded the actions that the observer budgerigars carried out on the same apparatus. They found evidence that observers were influenced by the particular demonstration they had seen, in terms of their preferred method of accessing the food reward.

Andrew Whiten and Deborah Custance (Whiten, Custance, Gómez, Texidor, & Bard, 1996) applied the two-action method in order to test for imitation in chimpanzees, using a piece of apparatus that they referred to as an "artificial fruit" (see Figure 9.1). The artificial fruit did not physically resemble a fruit, but it was designed to represent a logical analogue of foraging behaviour. It was simply a box with a hinged lid, and various latches that held the lid closed. When the artificial fruit was presented to animals in experiments, it was always presented with a food reward contained inside. In
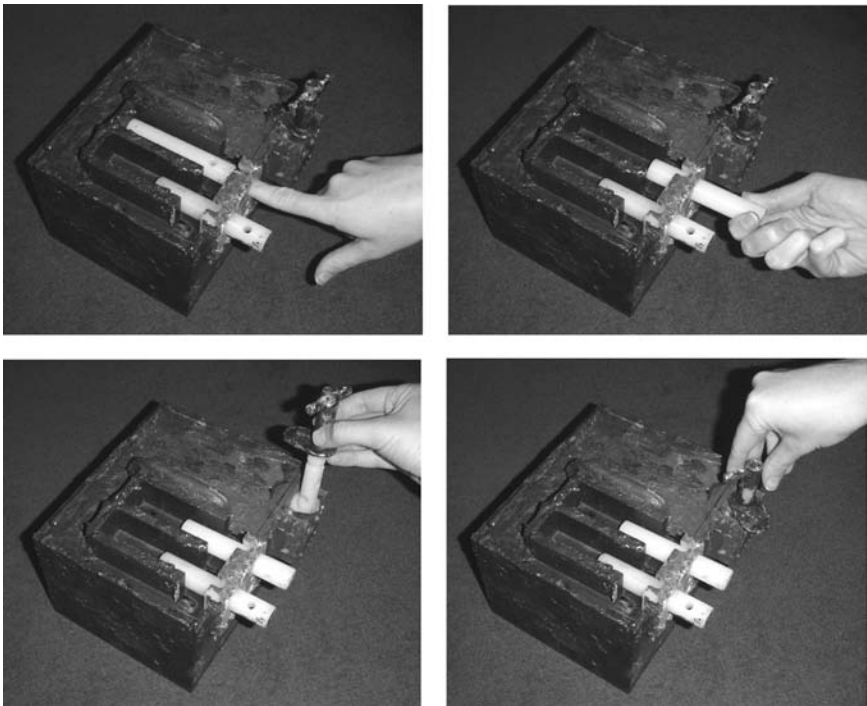
Figure 9.1 An artificial fruit. The bolts can be poked through (top left) or twisted out (top right), and the handle can be lifted out (bottom left) or turned (bottom right).

order to access the food reward, the latches therefore had to be released in order to free the lid. This resembled the kind of processing that nonhuman primates sometimes have to carry out on foods within their natural diet (such as nuts, or some fruits), in order to access an edible centre.

Embracing the logic of the two-action design, the artificial fruit had been designed such that there was more than one possible method of removing the latches. Sliding bolts could be either poked through from front to rear, or pulled or twisted out from rear to front. Another latch could be either rotated to free the lid, or lifted out altogether (see Figure 9.1). The chimpanzees were exposed to a human demonstrator performing one or other of the alternative actions on each of the latches, and were then presented with the artificial fruit themselves. The subjects that had seen twisting of the bolts produced more twisting-like actions, and those that had seen poking produced more poking-like actions.

The artificial fruit had deliberately been designed in such a way that it could be used to test for imitation in a variety of species, and since the original chimpanzee study, the method has also been used with gorillas (Stoinski, Wrate, Ure, & Whiten, 2001), orangutans (Custance, Whiten, Sambrook, & Galdikas, 2001; Stoinski & Whiten, 2003), capuchins (Custance, Whiten, & Fredman, 1999), and marmosets (Caldwell & Whiten, 2004), as well as parrots (Huber, Rechberger, & Taborsky, 2001) and adult humans (Horowitz, 2003). The logic of the two-action design was also used in Voelkl and Huber's (2000) study on imitation in marmosets, although in this case a photographic canister was used, which was opened by a monkey using either their hand or their mouth.

Group diffusion experiments

The problem with some experimental tests of social learning in primates is that they may not accurately simulate the conditions under which learning occurs in the animals' natural environment. Although we can readily demonstrate that primates *can* learn by observation, a question still remains about whether this kind of learning could result in the sort of group-specific behaviours that we observe in the field. Galef (1995) and Heyes (1993) have both argued that social learning will interact with individual learning in such a way that groups will inevitably converge on behaviours that result in the greatest reinforcement compared with alternatives. Between-group variation in behaviour is therefore unlikely to be supported by social learning. Heyes (1993) cited Galef, Manzig, and Field's (1986) replication of Dawson and Foss's (1965) study on budgerigars: Subjects that observed conspecifics accessing hidden food using either their beak or their foot tended to match the demonstrated technique for only the first two trials postdemonstration. In later trials, the difference between the groups disappeared.

However, other approaches to investigating social learning in primates have used designs in which whole groups are tested, rather than individuals.

Behaviour is also typically recorded over longer periods of time in these studies. Since the aim of such approaches is essentially to induce a tradition within a group, they therefore provide a more accurate indication of whether group-specific behaviours can be supported by social learning.

A number of experiments of this type have been targeted towards documenting the spread of a novel behaviour within a single social group (Huffman & Hirata, 2004; Tonooka, Tomonaga, & Matsuzawa, 1997). The problem with these designs is that it is difficult to establish the role of social learning, in the absence of a comparison group. Ideally more than one group would be compared, with each having been exposed to a different behaviour. In this way it would be possible to determine whether contrasting cultures could actually be generated. Whiten, Horner, and de Waal (2005) did exactly this, combining the two-action method with a group diffusion design. Two demonstrator chimpanzees, one from each of two social groups, were trained to perform a tool-use task, each using a different method from the other. The demonstrator chimpanzees were then introduced back into their groups, along with the apparatus on which they had been trained. Each performed the version that they had learned, and subsequently, there was a clear tendency for their group members to use the same method. The variation between the two groups was maintained over several days of testing, during which the apparatus was available to the chimpanzees for a total of 36 hours. This study effectively showed that social learning in primates does have the capacity to support behavioural variation, as the researchers showed that these alternatives were maintained over time within the two social groups.

Curiously, in a direct attempt to replicate Whiten et al.'s (2005) study, Hopper et al. (2007) found that two groups of chimpanzees showed a preference for the same method, even though one group had been exposed experimentally to the alternative. They attribute this to differences in the previous experiences of the two populations in question. The chimpanzees studied by Hopper et al. had extensive experience of enrichment devices which made use of a similar action to the one which was eventually preferred by all members of this population.

Price and Caldwell (2007) carried out a similar experiment with a zoo population of colobus monkeys. Our two-action task involved a box with a clear flap which could be either pushed or pulled to access a food reward inside. The population consisted of two separately housed groups of this species, so these two groups could be exposed to contrasting versions of the demonstration. The demonstration was in this case provided using video footage of another monkey performing the behaviour. The video presentation, whilst sacrificing some ecological validity, allowed for a high level of control over the demonstration, which can potentially be something of a problem in these naturalistic group designs. Price and Caldwell found that, whilst the demonstration footage was playing, subjects showed a high degree of matching to the demonstration (up to 100% matching for some subjects). Furthermore, the variation between the groups was sustained even after the

footage was no longer playing. There was still a statistically significant difference in the behaviour of the groups 5 days after the final presentation of the demonstration footage. Figure 9.2 displays the data from this study.

Interestingly, the pull group continued to prefer their demonstrated technique, despite this possibly being a less efficient method. For the subjects tested, the pull technique involved a bimanual manipulation of the apparatus, with the monkeys pulling the flap with one hand, whilst reaching in for the food reward with the other. Pushing, by contrast, was achieved with a single hand. It seems then that pullers may therefore have been disadvantaged by their technique, yet three of the four monkeys in the pull group continued to pull significantly more than push through all of the sessions. One particular individual, Scragg (see Figure 9.2), used both techniques roughly equally, and therefore had ample opportunity to learn about the relative effectiveness of the two techniques. However, even this individual continued to make use of the pull technique right up to the final test session.

It is particularly interesting to note that in similar test for social learning in monkeys, which used a dyadic rather than a group design, subjects rapidly converged on one preferred method (Bugnyar & Huber, 1997). Bugnyar and Huber used a push/pull task similar to that used by Price and Caldwell (2007), but found that the initial preference of observers of the pull demonstration disappeared over the course of five test trials, with all subjects converging on the push alternative.

There are clear differences between the two studies, which make it difficult to draw any strong conclusions about the reasons for the contrasting
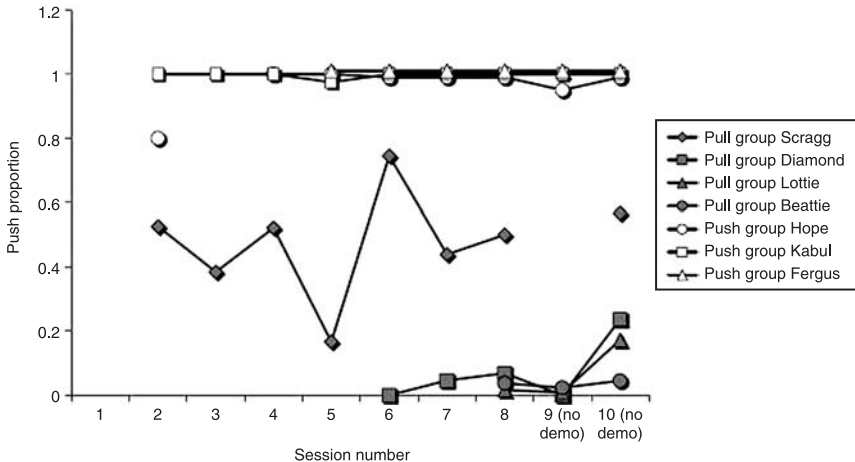
Figure 9.2 Proportion of pushes to pulls for each subject, for all sessions. Demonstration clips were shown during sessions 1–8, which were each held on successive days. Session 9 was held 24 hours after the demonstration footage had last been shown, and session 10, 5 days later. Redrawn from Price and Caldwell (2007).

outcomes. Bugnyar and Huber (1997) tested marmosets, a small New World monkey, and Price and Caldwell (2007) tested colobus monkeys, a larger Old World monkey, and there are clear behavioural and morphological differences between the two species. Furthermore, there are minor differences in experimental method other than the use of a dyadic versus a group design (and of course a similar contrast in outcome was found between Hopper et al. (2007) and Whiten et al. (2005) cited earlier, despite virtually identical methods, which suggests that such differences in outcome may sometimes be attributable to extremely minor variations in procedure or population). Nonetheless, Price and Caldwell's findings raise the intriguing possibility that testing for social learning in groups may increase the time taken for behavioural variants to extinguish, compared with testing isolated individuals. The actions of group members may function as repeat demonstrations, influencing individuals to persist with a particular behaviour, and counteracting the effects of their own experience through trial and error. This is currently an extremely speculative suggestion. In order to test this, one would have to compare conditions in which subjects were tested either individually or in a social group, in order to find out in which of these conditions the socially learned variants corrupted more rapidly. However, research along these lines may provide crucial insights into how between-group variation can be supported by social learning, despite the influence of trial-and-error learning.

Transmission chain experiments

The strength of group diffusion designs lies in their close simulation of natural learning conditions. However, the corresponding disadvantage of this is that little control is possible, following the initial introduction of a behaviour into the group or groups. In transmission chain designs, far greater control is possible, in terms of manipulating certain variables that may affect learning. Another benefit of this approach is that it may provide a better analogue of intergenerational learning, as this is in effect what such designs attempt to simulate.

Transmission chain designs involve the systematic replacement of individuals in controlled laboratory groups such that one-time learners become the demonstrators for later subjects. These approaches have been used to good effect with rats (Galef & Allen, 1995; Laland & Plotkin, 1990), birds (Curio, Ernst, & Vieth, 1978), and fish (Laland & Williams, 1997, 1998), as well as nonhuman primates. The first example of this approach being applied to animals was Menzel, Davenport, and Rogers' (1972) study of chimpanzees' responses to novel objects. Menzel et al. were interested to discover whether neophobic responses could be overcome by observing conspecifics interacting with novel objects, and if so, whether this could potentially lead to traditions of avoiding or approaching particular objects. Menzel et al.'s study population consisted of 19 chimpanzees. At any one time, a total of three of these chimpanzees were housed together in the same

enclosure and tested together with the target objects. However, every 2 months the researchers would replace the longest-standing member of this trio with a new individual from the population. So, by the time the fourth trio was created (consisting of the fourth, fifth, and sixth members), the original founder members of the group (i.e., the first, second, and third) had been completely replaced. Menzel et al. found that the first and second trios avoided both of the test objects, but one member of the third trio habituated to one object and began interacting with it, and one member of the fifth trio likewise habituated to the other test object. Subsequent trios would then interact with these objects, continuing the "play" tradition, even once the originator had left the group. Menzel et al. concluded that the ways in which the chimpanzees responded to the objects was characteristic of the group, rather than being idiosyncratic.

Horner, Whiten, Flynn, and de Waal (2007) used a transmission chain design with a two-action task, in an attempt to create two contrasting cultures in chimpanzees. Initially, two individuals were trained to obtain food from a foraging device, each using a different method. These trained chimpanzees provided the demonstration for the next individuals in the chains. Then, the responses of the observers were used as the subsequent demonstration for the next individual, and so on. One version was passed along a chain of five chimpanzees, and the other along a chain of six. In both cases, transmission was virtually perfect, with 10 of the 11 subjects exclusively using their chain's original method. This finding strongly supports the idea that contrasting behavioural traditions can be sustained through social learning, over multiple generations.

EXPERIMENTAL APPROACHES TO THE STUDY OF CULTURE IN HUMANS

So, to date, experimental research on culture in nonhuman primates has made use of a variety of methodologies, and the results raise intriguing issues of broad-ranging consequence regarding how, when, and why particular behaviours may be sustained within groups by social learning. In this particular field, therefore, there is much that can be learned from the literature on nonhuman primates, in terms of augmenting our understanding of our own species.

In the current scientific literature, there are a great deal of examples of experimental tests of social learning in humans, but the vast majority of these make use of simple dyadic designs (too many to review here). Few have exploited designs involving naturalistic groups, or transmission chains. This is quite surprising, given how informative such approaches could potentially be. Interestingly, the studies of this type that do exist are fairly scattered throughout the literature. This dispersal is apparent in terms of where such research has been published, as examples can be found in a variety of specialist

journals from a number of different disciplines. It is also apparent in terms of when it was published; such approaches have been used for at least 70 years, and yet there is no clearly identifiable period of popularity. Therefore (although this is not intended to be an exhaustive review of this area of research), the aim of this section is to introduce the reader to the predominant approaches within this field, as well as some of the more intriguing findings.

Overlapping replacement microcultures

Several studies with humans have employed the same methods used by Menzel et al. (1972), and other researchers (Galef & Allen, 1995; Laland & Williams, 1997, 1998), with animals. These studies have all created multiple overlapping "generations" of learners, by establishing small groups of subjects that are individually removed and replaced by new members.

Jacobs and Campbell (1961) used this approach to good effect, in order to determine whether participants' tendencies to conform to majority opinion could result in long-lasting traditions within groups. Participants were asked to estimate the degree of movement of a point of light in a dark room (in fact the light did not move at all, but the perception of a small amount of movement is a persistent and reliable illusion). Groups ("microcultures" in their terminology) were founded by experimental confederates, instructed to respond with a significant overestimation of their true perception of the degree of movement. The responses of naïve participants who joined the group of confederates were swayed in the direction of the confederates' answers, compared with a control group without confederates. However, what was more interesting was that the bias towards overestimation remained, even as the confederates were gradually replaced with naïve participants. Responses of experimental groups continued to be significantly higher than those of control groups for four generations after the final confederate had been removed.

It is worth noting though, that the overestimation bias showed a rapid decline over generations. A very strong bias was induced in early generations, stimulated by the responses of the confederates, but this effect dropped off sharply as soon as confederates began to be removed, and continued to do so until responses between experimental and control groups were statistically indistinguishable (five or six generations after the final confederate was removed). Jacobs and Campbell (1961) in fact conclude that:

> the outcome may well warn us against the assumption that a purely arbitrary cultural norm could be perpetuated indefinitely without other sources of support. Even if people weigh the opinions of their elders many times that of their own direct observations, the collective effect of their own observations probably soon erodes a *functionless* arbitrary belief.
>
> (p. 657, italics in original)

Weick and Gilfillan (1971) extended upon Jacobs and Campbell's (1961) findings. They believed that arbitrary traditions could in fact be perpetuated within groups, as long as the traditions were not (in their terms) "unwarrantedly" arbitrary. In other words, they believed that particular behavioural alternatives could persist, as long as any differences between the alternatives was essentially inconsequential. They asked group participants to play a game, the aim of which was to produce numbers that added up to a particular sum decided by the experimenter. Participants were not permitted to communicate, and therefore success on the game depended on having an agreed strategy. Many possible strategies could lead to success in the game, but founders of some groups were instructed in the use of one that was very easy, involving little mental arithmetic, whilst others were instructed in the use of one that was very difficult, requiring quite complicated calculations. After four generations, the difficult strategy was being used no more than it was by a control group who had received no instructions. However, the groups that had been instructed in the use of the easy strategy continued to use this method much more frequently than the control group did, right up until the end of the experiment (11 generations).

   Similar methods have also been used by Insko and colleagues (Insko et al., 1980, 1983) and, more recently, by Baum, Richerson, Efferson, and Paciotti (2004). The value of this method for Inkso et al. (1983) lay in its capacity for experimental manipulation. They were able to test competing hypotheses about the reasons for the emergence of leadership in human societies, by creating microcultures that operated under different governing rules. Thus, theoretical debates that were difficult to address on the basis of anthropological and archaeological data could be tackled by recreating hypothetical historical societies in miniaturized form under laboratory conditions. For Baum et al. the microculture method offered a window into the process of cultural evolution, illustrating how it can lead to adaptive strategies.

Serial reproduction

The "Method of Serial Reproduction" was first used by Bartlett (1932) in his studies of human memory. What this approach has in common with the microculture research is that chains of multiple generations are involved, with participants learning from previous learners. However, it is quite different in a number of other important respects. First, and perhaps most importantly, in this type of research, participants are explicitly instructed to copy, in that their aim is to reproduce information as accurately as they possibly can. In contrast, in microculture studies, participants are never instructed to copy other members, but rather such effects emerge spontaneously. During serial reproduction tasks, participants may also never meet one another, but, rather, written material is passed on by an experimenter. Indeed, participants may never even be aware of their role as a member of a transmission chain. This

contrasts strongly with the microculture approach in which social interaction and coordination tend to be all important.

The benefits of serial reproduction tasks lie in their ability to reveal people's unconscious cognitive biases, as they allow researchers to investigate what sort of information is omitted, or introduced, when participants are actively trying to reproduce material as accurately as possible. Bartlett (1932) used the method to show that stories passed on in this way were, over several generations, gradually influenced by participants' cultural backgrounds. Chains of Indian and English students were found to pass on somewhat different versions of the same story. The method has also been recently revived by Mesoudi and colleagues (Mesoudi & Whiten, 2004; Mesoudi, Whiten, & Dunbar, 2006), who have used it to illustrate people's biases towards hierarchical structure in event descriptions (Mesoudi & Whiten, 2004), and also their tendencies to preferentially reproduce social, as opposed to nonsocial, information (Mesoudi et al., 2006).

Other approaches

A number of other experimental approaches have been taken that do not fit neatly into either of the two categories just discussed. For example, Rose and Felton (1955) investigated how participants influenced each other's interpretations of Rorschach inkblot cards. Their design had similarities with the microculture method, but, rather than using successive generations, individuals moved between three different groups, so the researchers could observe how ideas spread from group to group. Schotter and Sopher (2003), meanwhile, investigated how game strategies were influenced by word-of-mouth advice between nonoverlapping generations of individual players.

A particularly interesting experiment by Garrod and Doherty (1994) used repeated dyadic interactions between a restricted pool of participants in order to show how linguistic conventions can be generated and maintained. In Garrod and Doherty's experiment, participants were asked to play a game that required a certain amount of communication and coordination between two players. Participants who played the game repeatedly with the same partner were compared with those who played the game repeatedly with multiple different partners, all of whom had also been playing the game with other members of the same group. In playing the game, participants needed to describe a maze to one another, and a number of possible alternative schemes could be used to describe locations. Garrod and Doherty found that, initially, the isolated pairs showed a higher degree of convergence in terms of the descriptive schemes they adopted. However, further down the line, when more games had been played, the group began to show a higher level of convergence than the pairs. Garrod and Doherty argue that, once conventions were established, these were adhered to more strongly by the group than by the isolated pairs, as the isolated pairs could more readily update their schemes on the basis of previous interactions.

A final, recent, study merits mention. Salganik, Dodds, and Watts (2006) took a very different approach to the experimental study of culture than any of the other studies cited here. They were interested in how information about other people's preferences affected consumer choice. They hypothesized that popularity can be self-perpetuating, in that the more a particular product is selected, the more likely it is to be selected by further individuals. In order to test this hypothesis, they created a virtual music market, in the form of a website where unknown songs could be downloaded. However, potential consumers were directed to one of a total of eight isolated cultural markets, all of which offered exactly the same products. Within each cultural market, information was available regarding which songs had been most frequently downloaded by others. These cultural markets were also compared with a noncultural market, in which the information about others' downloads was not provided. What they found was that, although certain songs did well in all markets, and others poorly, success was nonetheless relatively unpredictable. The eight isolated cultural markets each showed different patterns of popularity, and these were only weakly related to quality (as measured by success in the noncultural market). The multiple simulated worlds of this experiment demonstrate brilliantly how divergent cultures can materialize spontaneously, and even self-perpetuate.

Taken together, these individual pieces of research allow us to draw some insightful conclusions about cultural transmission. For example, it is clear that arbitrary traditions can in fact be perpetuated, under a variety of circumstances. As Weick and Gilfillan (1971) showed, if alternatives are truly arbitrary, in the sense that any differences are fairly inconsequential, then arbitrary culturally transmitted variation can surely be maintained. Also, if there is some value in convention (as there is in communication, as one must make oneself understood to others), then initially arbitrary conventions are likely to stabilize and be maintained, as shown by Garrod and Doherty (1994). Finally, if social learning is considerably less costly than individual learning (as it was in Salganik et al.'s, 2006, experiment, due to the fact that looking at the download information was much quicker than listening to each song individually) then, likewise, cultural variation can readily emerge between groups.

CONCLUSION

Recent, high profile, research on culture in nonhumans (in particular non-human primates) has helped to highlight the value of similar research with humans. Although there is already existing research taking an experimental approach to the study of culture in humans, the examples are somewhat scattered throughout the literature. Furthermore, it is quite surprising that at no time have such approaches appeared to take off in terms of popularity (other than, just possibly, right now). It is perhaps ironic that there is no

clearly identifiable tradition within the science of human traditions. However, the research within this area has much to offer, and it is clear that there are many promising avenues for future research in this area. The literature on culture in nonhuman primates is currently only beginning to address questions regarding how cultural behaviours might be maintained within groups, given the influence of individual learning. But the literature on social learning in humans is really starting to offer some answers. The recent excitement surrounding research on culture in nonhuman primates will, with any luck, serve to draw attention to some of these studies with humans, and encourage further work of this kind.

ACKNOWLEDGEMENTS

10 How the chimpanzee stole culture, or lessons learned from labours in cultural primatology

William C. McGrew

The idea that living species other than *Homo sapiens* might be cultural dates at least to Morgan (1868), who championed the beaver as a candidate for culturebearer. In the social sciences, academic engagement with the possibility of animal culture cropped up fleetingly throughout most of the twentieth century. An early example was Kroeber's (1928) response to reading of the intellectual feats of captive chimpanzees, in Koehler's (1927) monograph, *The Mentality of Apes*. Kroeber devised a list of six criteria, which if met by the apes, would convince him to grant them cultural status. Both died before the age of modern field primatology, but their views were prophetic.

Serious debate on the topic arguably began when Menzel (1973) organized a symposium on "primate precultural behaviour" at the fourth International Congress of Primatology, where Goodall (1973) made a typically astute contribution. My introduction to the debate came with an article published in *Man* (McGrew & Tutin, 1978), after which we were immediately broadsided by two distinguished anthropologists, one biological and one cultural (Washburn & Benedict, 1979). The "chimpanzee culture wars" have been going on ever since (McGrew, 2003); for a recent, heated exchange about culture in nonhumans, see Laland and Janik (2006, 2007) and Kruetzen, van Schaik, and Whiten (2007).

I wrote a book (McGrew, 2004) on the subject, and included a chapter of 20 lessons learned from more than three decades of studying wild chimpanzees (see Table 10.1). Here I add another 10 lessons, based on further contemplation and new data. Finally, I do not wish to insult either the wonderful Dr Seuss (1957) or my equally wondrous fellow apes by likening a chimpanzee to a grinch, but the titular catchphrase is irresistible.

HUMAN CULTURE IS UNIQUE, BUT SO IS _____.

Fill in the blank! Equally unique is human locomotion, foraging, social organization, sexuality, intellect, and worldview. But the same applies to chimpanzee culture, locomotion, foraging, etc. Ditto for dolphin, garter snake, or cockroach. That's what makes them separate species, a point made

Table 10.1 Twenty pithy epigrams, or lessons learned from 30 years of chasing wild chimpanzees and seeking to understand their culture (McGrew, 2004)

 1. Define culture as you wish, just make it operational.
 2. Labels are less important than content.
 3. Culture as checklist—recipe for disappointment.
 4. Don't wait to know "how" before you ask "what", "where", "when", "why", etc.
 5. Be sceptical of both Humanists and Universalists.
 6. Don't buy the space shuttle argument.
 7. Avoid anthropomorphism and anthropocentrism.
 8. Nature and nurture provide the context, but not the shackles.
 9. Between-group variation and within-group similarity prove nothing.
10. Start with material culture, but don't stop there.
11. Beware of anecdotes but don't ignore them.
12. Raid socio-cultural anthropology, selectively.
13. As with humans, there is diversity in chimpanzee culture.
14. Engage with archaeologists—they have similar problems.
15. Experiments are wonderful, but hard to do.
16. Social learning is the starting point, not the end.
17. Tradition and culture are a mess.
18. Language may be a red herring, or worse.
19. Teaching is the last resort, or even a poisoned chalice.
20. Culture is a curse as well as a blessing.

convincingly in the context of human evolution in a cleverly titled book by Robert Foley (1987).

In nature, every creature is unique (as even identical twins differ phenotypically) and none is unique (as we are all constructed of the same four nucleotides). A more interesting (if ultimately illogical) way to tackle the problem of comparison is the sometimes-claimed differences in degree versus kind. If two phenomena are not the same, are their differences qualitative, or only quantitative? Are they variations on a theme, or wholly different themes altogether?

The anthropocentrist finds this easy: No nonhuman species ever produced a laptop computer, much less an abacus. Therefore, humans are computationally unique. But what of those preliterate human societies whose number systems lack even arithmetic? And what about those laboratory apes that can add and subtract? Given these complications, either those traditional human societies have to be excluded from humanity (for lacking the abacus, etc.), or, humans can be compared with nonhumans only on universal traits. (Human universals are traits shared by all *Homo sapiens*, even if they are nuanced in local diversity; Brown, 1991.) Or, perhaps there are no real differences in kind but only degree between hominine species?

The lesson is not to quest for a Rubicon in seeking to distinguish human culture from nonhuman culture, but instead to accept diversity with continuity. Another way of putting the same argument is to make the null hypothesis one of continuity rather than discontinuity. That is, assume first that humans

and nonhumans share attributes until shown otherwise, rather than the anthropocentric reverse.

ENCULTURATION VERSUS ACCULTURATION—DOES IT MATTER?

How does a naïve organism become cultured? One way is to grow up normally, in a society, and be the recipient of experientially acquired knowledge. This is called enculturation and is a developmental (ontogenetic) process; in psychology, it is called socialization. Another way is to be introduced to or immersed in an alien culture, and acquire information from that exposure. This can happen at any age, and there is no need to posit critical periods, although there may be sensitive stages (cf. language acquisition). A legitimate question arising, however, is how alien is alien?

In cultural primatology, field researchers typically study enculturation (apes rearing apes), but laboratory researchers may study acculturation (humans rearing apes). This can cause confusion, as the latter amounts to artificial cross-fostering, in which human caretakers rear (to varying degrees) apes in human environments (zoo, lab, safari park, household), sometimes from birth. Perversely, no one ever does the reverse acculturation (except in Tarzanic fiction), as human infants are not fostered to surrogate ape mothers. However, enculturation can be studied in captivity, in naturalistic settings in which ape parents embedded in social groups are allowed to rear their offspring (de Waal, 2001). Similarly, acculturation can be studied (at least to a limited extent) in free-ranging primates, via ethnoprimatology, e.g., in crop-raiding.

How much does it matter which we study? In one sense, in an increasingly human-dominated world, all environments are now artificial, and few vertebrates any longer live in their environment of evolutionary adaptedness. On the other hand, wild creatures have to worry about competitors, predators, prey, hazards, etc., but captive ones do not. In nature, both successes and failures have consequences, sometimes even fatal ones, while captive animals are largely buffered from such selection pressures. Ultimately, adaptation in the broadest sense is about surviving and thriving in the setting that you inhabit, however unnatural it may be. If culture transcends nature, then why limit observational or experimental cultural primatology to wild populations? The lesson is that process matters more than context.

ANTHROPOLOGY DOES NOT OWN THE CULTURE CONCEPT

There was a time when the discipline of anthropology was grounded on the culture concept (Kuper, 1999; Sidky, 2004). Having invented it, anthropology

claimed priority, and so, jurisdiction. That monopoly may have worked when only human beings were studied, but with other species now in the picture, the horse has long since left the stable, so there is no point in trying to shut the door to other disciplines.

As discussed elsewhere (McGrew, 2003, 2004), the strengths and expertise of several disciplines are needed to explain culture both across and within species. This is because different disciplines tend to ask different questions: *Anthropology* tends to ask "what" questions about culture as phenomenon. *Psychology* tends to ask "how" questions about culture as mechanism. *Biology* tends to ask "why" questions about culture as adaptation. *Archaeology* tends to ask "when" questions about culture as timeline. All of these, and more, are needed for a satisfactory synthesis. Of course, interdisciplinary efforts have been made before (e.g., "cultural materialism"; Harris, 1979), but not by primatologists. Ironically, just when the study of culture has opened up to include nonhumans, some anthropologists prefer to abandon the concept (Kuper, 1999). This seems a shame, especially if, although denying it, they refuse to allow anyone else to have a go at making it work (e.g., Ingold, 2001).

The lesson is for cultural primatologists to learn from the past and present successes and failures of sociocultural anthropology, but not be limited by either.

DEPENDENCY IS NOT THE ISSUE

A common claim in introductory textbooks for human cultural uniqueness is that only humans depend on culture; for other species, if it exists, it is only an optional extra. Thus, we are impressed that wild chimpanzees have some elementary technology, but we think that they could do without it, like other animals.

The argument is specious, however often it is asserted. Consider the logic: All human societies have culture. Since we cannot find a noncultural exception to the rule, then humans must depend on culture. But the same logic applies to chimpanzees: All chimpanzee communities also have culture, e.g., in the form of elementary technology. (Strictly speaking, some populations of apes that have been studied only briefly have yet to show material culture, but all that have been studied long term do; McGrew, 1992, 2004.) Therefore, chimpanzees are equally dependent on culture, at least on grounds of ubiquity.

Of course, there are other criteria for measuring dependency. It is often pointed out that humans are able to occupy inhospitable environments because of their material culture. The same applies to chimpanzees on hot, dry, and open savannas, e.g., apes that dig wells for drinking water and use leafy sponges to extract the water, in the dry season (Hunt & McGrew, 2002). The lesson is not to depend on dependency.

NOT EVERYONE HAS PERFECT PITCH, BUT WE ALL DRINK COKE

In the nature versus nurture debate, there is a tendency to equate nature with genetic determinism and nurture with cultural relativism. In this dichotomy, genetic means fixed and invariant, while culture means plastic and variable. This contrast is simplistic, as all sensible scientists are interactionists (Ridley, 2003).

However, in seeking to explain human culture, it is easy to focus on nurture and ignore nature, given such rich behavioural diversity within *Homo sapiens*. Sometimes forgotten is that variation can be primarily genetically determined and uniformity can be culturally determined.

Perfect pitch, as manifest in glorious solo or choral singing, is primarily genetically determined (Tramo, 2001). The rest of us can take singing lessons all our lives but may never attain what someone else was born with.

Worldwide consumption of sweetened, carbonated, cola-flavoured beverages is culturally determined ("I'd like to buy the world a Coke!"). Its invention and rapid dissemination is well-known, but an extraplanetary ethnographer arriving now to find its ubiquity could be forgiven in classing it among the other human universals such as incest avoidance, maternal infant care, burial rites, etc. (Brown, 1991). The lesson is to apply the same avoidance of presumption to explaining variation or lack of it in nonhuman primates, as we do in humans.

NONHUMANS RATCHET, TOO

A prominent candidate for a distinguishing feature of uniquely human culture is the "ratchet effect" (Tomasello, 1994). It is said that only humans show additive, incremental improvement in their cultural acts, so that each generation stands on the shoulders of its predecessors, building on their cumulative legacy. This sounds good, especially for advanced technology, e.g., change from buggy to Bugati. Nonhuman species are said to lack this ability to make collective, cumulative advances.

Putting aside issues of naïve progressivism, there are practical problems with this viewpoint. First, detecting adaptive change in long-lived, slowly reproducing organisms, such as apes, in the course of a study lasting only years instead of decades, is not realistic. Most field chimpologists have never seen an innovation, much less its adoption as a societal norm. But by the same token, most ethnographers of traditional peoples also have never seen ratcheting; to trot out the old saw, "Absence of evidence is not evidence of absence", especially if the time-frame for data collection is too brief.

However, an easier refutation for Tomasello's (1994) claim comes from published evidence of ratcheting in living nonhuman primates. The Japanese monkeys of Koshima, an island in southern Japan, have been studied since

1948. Their invention and dissemination of new food processing habits, such as sweet potato washing (Kawamura, 1959) and wheat sluicing (Kawai, 1965) appears in every introductory textbook in anthropology. However, secondary accounts inexplicably present these customs as frozen in their original form, circa the 1950s. Actually, the food-processing techniques have been ratcheting for decades (Hirata, Watanabe, & Kawai, 2001; Kawai, Watanabe, & Mori, 1992; Watanabe, 1994). Monkeys shifted from washing their tubers in fresh water to sea water, apparently to add a salty taste. Monkeys moved their sluicing spots from the waves breaking on the shore to purpose-dug pools on the beach, apparently to gain more control over the process.

The lesson is to be cautious of drawing negative conclusions that neatly fit prevailing, pessimistic preconceptions.

DIRECTIONAL TRANSMISSION—EVERY WHICH WAY?

Cultural transmission flows from individual to individual, which seems simple enough, but, despite incisive treatment of the possibilities (e.g., Richerson & Boyd, 2005), the actual processes remain enigmatic.

For example, one-to-one transmission is easy enough to see in nonhuman primates, but what about many-to-one (as in, "it takes a village to raise a child") or one-to-many (as in a charismatic guru)? And who exactly is the "many"? It could be family, clan, community, or even population, depending on dispersal patterns. (This also raises the point of when dissemination becomes diffusion.) Even one-to-one is not so simple, if the opposite-sexed parent does not join in childrearing. Chimpanzees largely grow up in one-parent, matrilineal families, so how could a male chimpanzee learn how to be masculine from his mother?

Similarly, it is easy enough to classify information transmission as vertical (= across generations, along lines of direct descent), oblique (= across generations, but beyond lines of direct descent), or horizontal (= within generations, with descent being irrelevant). But what about direction? For vertical and oblique, transmission is usually assumed to be from older to younger, but some of the classic cases, e.g., sweet potato washing in Japanese monkeys, were from offspring to mother (Kawamura, 1959).

Finally, what is a generation, in cultural terms, in which the ideas (unlike genes) are not limited by meiosis? In long-lived creatures, it is not uncommon for an uncle to be the same age as his nephew, so are they of the same or different generation? Humans may organize their cultural generations by cohorts, e.g., the *morani* of the Maasai, but who has looked at this in non-human species? Or, what to make of Opie and Opie's (1987) finding that children's games such as skipping rope chants may be passed down for centuries by peer transmission. Is this vertical or horizontal transmission? Or what if knowledge is acquired from an older sibling, is this oblique or vertical? The lesson is that information flows, but unlike water, it may run uphill.

LIKE MOST OTHER THINGS EVOLUTIONARY, CULTURE IS BUSHY

Anagenesis rarely accounts for speciation, and it seems likely to be true for cultural differentiation too. Although there is a tendency to think in terms of grades (lemur–monkey–lesser ape–great ape) that lead us into simple-minded hierarchical structures, ethnography tells a different story. Although more than half the publications in culture primatology come from one genus, *Pan* (chimpanzee and bonobo), the deepest and broadest other datasets are from monkeys, especially *Macaca* (macaques) and *Cebus* (capuchins) (McGrew, 1998). Many parallel features, from medicinal plant use to social hunting, have converged in the chimpanzee and the white-faced capuchin monkey, showing cladogenesis for simian culture. Similarly, convergence in lithic percussive technology is striking in monkeys, between New World capuchins (Moura & Lee, 2004) and Old World macaques (Malaivijitnond, Lekprayoon, Tandavanittj, Cheewatham, & Hamada, 2007).

Furthermore, cultural primatological analysis is multilevel, so that comparison must be made with care. At species level, both bonobo and chimpanzees show branch dragging in display, but these appear to have different functions (meanings?) for these sibling species. At subspecies level, far western chimpanzees (*Pan troglodytes verus*) crack nuts while their eastern counterparts (*Pan t. schweinfurthii*) do not, though both have access to nuts and to tool raw materials (McGrew, Ham, White, Tutin, & Fernandez, 1997). At population level, Gombe chimpanzees dip for army ants using a two-handed, pull-through technique, while Tai chimpanzees use a one-handed, direct mouthing technique, and Bossou chimpanzees do both (Schöning, Humle, Möbius, & McGrew, 2008). At group or community level, neighbouring K-group and M-group at Mahale show nuanced variants of the grooming-hand-clasp (McGrew, Marchant, Scott, & Tutin, 2001; Nakamura, 2002). Variation also exists at the lineage (Lonsdorf, 2005) and individual levels, but these seem more akin to subcultural or idiosyncratic differences. The lesson is that there is no Great Chain of Being for culture, any more than there is for any other phylogenetic trait.

CULTURE IS MORE THAN BY DEFAULT

If culture must be socially learned, then behavioural patterns that are acquired in other ways cannot be cultural. Thus, behaviour resulting solely from genetic or nonsocial environmental causes does not count, even if it is learned individually (e.g., by trial and error) while in a social setting. In primatology, these distinctions were made more than three decades ago by Kummer (1971). This trichotomy is simple in principle, but difficult in practice, as nature and nurture usually are not extricable (Ridley, 2003). The only way to disentangle them conclusively is through careful experimentation that

controls for all other independent variables, e.g., cross-fostering of mono-zygotic siblings. Such studies are neither ethically nor logistically realistic in primates.

So, field workers in cultural primatology collect data as systematically and carefully as possible, noting genetic and environmental variables as well as they can, as well as keeping track of the ontogeny of known individuals, whenever possible (e.g., Lonsdorf, 2005). They draw comparisons across groups, at levels ranging from families to subspecies, noting commonalities and contrasts. Obviously, the more detailed and comprehensive these comparisons, the more likely are their inferences to be sound. However, logically, their interpretations about the causation of behavioural diversity (and uniformity) and the extent to which it is cultural can never be conclusive, as all possible variables can never be controlled in nature. Instead, cultural primatologists can hope to draw inferences that are successively more accurate, with better and better data, and tighter and tighter arguments, as is the norm in science.

Critics of cultural primatology, mostly experimentalists who have never seen a wild primate, have seized on this limitation in field studies (e.g., Laland & Janik, 2006). They have mislabelled it the "ethnographic" technique (thereby rendering it merely descriptive) or characterized it as the "method of exclusion" (thereby rendering it simplistic).

In reality, there seems to be no case of a cultural primatologist claiming that cultural behaviour is purely social, to the exclusion of genetic or environmental factors. To do so, for any organism, especially a long-lived, big-brained one, would be nonsense. Thus, the critics' argument is a straw man.

It is worth noting that under the criteria noted by the critics, none of the rich diversity in human action could be conclusively inferred to be cultural. The ethnographic record and sophisticated ethnological analyses of the sociocultural anthropologist do not meet experimental standards and so would be null and void.

The lesson is to tackle complex phenomena as best you can, but not to despair if the results are not 100% certain.

CULTURAL SURVIVAL APPLIES TO OTHER SPECIES, TOO

There is an organization called Cultural Survival that acts on behalf of indigenous, traditional human societies seeking to avoid being overwhelmed by global modernity. Its advocative publication, *Culture Survival Quarterly*, chronicles such extinctions in progress, e.g., the last stone axe makers of New Guinea are reduced to an ageing handful who still know how to make the tools, and there are no apprentices to carry on the custom (Stout, 2002). Already, many tribal languages have been lost, before they were ever set down by linguists.

Cultural Survival makes no mention of other species, but it could. When

populations, groups, or lineages die out, whether of sponging dolphins, or singing whales, they too are gone forever. Sometimes cultural salvage is possible, through relocation, rehabilitation, or reintroduction, or even, as a final resort, captive propagation. But these are desperate measures, far less preferable than proactive, preventative ones.

The lesson is that it is no longer enough for cultural primatologists to talk of preserving a species; instead, they must work to preserve a rich array of cultures (cf. Laiolo & Jovani, 2007).

CONCLUSIONS

To what extent the lessons listed here, plus those posed earlier (McGrew, 2004), are useful is for the reader to judge. In many ways, cultural primatology has reinvented cultural anthropology and has got so far to about 1960 in its reiteration (Borofsky, Barth, Shweder, Rodseth, & Stolzenberg, 2001). This is both good and bad. It is good because cultural primatologists have shown that combined ethnological and ethological analyses are a powerful allied tool to help explain a key phenomenon that extends beyond humanity. It is bad because some cultural primatologists retain a marked deference to a subdiscipline, sociocultural anthropology, many of whose practitioners reject the culture concept. One can only hope that efforts to build bridges across disciplinary chasms, as in this volume, will persist, to the enlightenment of all concerned.

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11 Great apes and the human resistance to equality [1]

Dale Jamieson

Questions about the nature and limits of the community of equals are controversial in both theory and practice. As I write these words, a bloody war between Serbs and Croats is continuing in the former Yugoslavia. Many fear that this is a preview of what may happen in what was once the Soviet Union. Tensions between Czechs and Slovaks are running high, and "the troubles" continue in the northern part of Ireland. Here in New York, where I am writing this chapter, relations between Hasidic Jews and African-Americans in the Crown Heights section of Brooklyn may have deteriorated to the point where a cycle of reprisal killings has begun. Relations between blacks and Koreans are generally very bad and all over America there are incidents of white racism against blacks and Asians.

Most people would express regret about all of these cases, and say that in the highly interconnected world in which we live different groups are going to have to learn to get along with each other. They don't have to like each other, but they must respect each other as equals. Whether Croat or Serb, black or Hispanic, all humans are members of the community of equals and have the right to live in peace and tranquillity, without threats to their lives and liberty.

The cases of interethnic struggle that I have mentioned pose practical problems of community: How can we bring it about that people will act on the basis of what they believe to be true and recognize the equality of others? At the level of theory the battle mostly has been won. Not many people would seriously argue that it is permissible to treat Serbs or Australian Aborigines badly on grounds of their race or ethnicity. But human beings are often better at theory than practice.

We have a long way to go even in theory towards recognizing our equality with the other great apes. The idea that chimpanzees, gorillas, and orangutans should be recognized as members of our community of equals strikes many people as bizarre or outrageous. Yet, like the other contributors to the Great Ape Project, I believe that we have very good reason for including them.

In this chapter I will not try to say specifically what the community of equals is or to what its members are entitled. Instead I simply endorse the general sentiments of the Declaration on Great Apes: The community of equals is the moral community within which certain basic moral principles

govern our relations with each other; these moral principles include the right to life and the protection of individual liberty (Cavalieri & Singer, 1993, pp. 4–7).

My main interest in this chapter is in exploring why the moral equality of the great apes is so difficult for many humans to accept. What follows can be viewed as a speculative diagnosis of the sources of human resistance to recognizing our moral equality with the other great apes. My hope is that once the sources of this resistance have been exposed, they will to some extent have been disabled, and we can then move towards the difficult task of putting our moral ideas into practice. I will discuss what I take to be five sources of resistance to recognizing our moral equality with the other great apes.

One source of our resistance may be this: We are unsure what recognizing our equality with the other great apes would mean for our individual behaviour and our social institutions. Would they be allowed to run for political office? Would we be required to establish affirmative action programmes to compensate for millennia of injustices? To some extent this unclarity comes from the narrowness of our vision, and to some extent because there are significant questions involved that cannot be answered in advance. Humans often seem to have failures of imagination when considering radical social change. A world without slavery was unfathomable to many white southerners prior to the American Civil War. Life without apartheid is still unimaginable to many South Africans. One reason we may resist radical social change is because we cannot imagine the future, and we fear what we cannot imagine.

But having said this, it is true that it is very unclear exactly what recognizing the moral equality of great apes would mean. Clearly it would end our use of chimpanzees in medical research, and our destruction of areas in which mountain gorillas live, but what other changes would it bring? We can benefit here from reflecting on the American experience of social change. Once slaves were emancipated and recognized as citizens, it remained unclear what exactly their rights and protections were. For more than a century various court decisions and legislative acts have continued to spell them out. This is an ongoing process, one that cannot entirely be envisaged in advance. If we are to change social practices that cannot be defended, then we must accept the unavoidable uncertainty that follows.

A second source of resistance may generally be connected to the sources of racism and sexism. Humans often tolerate diversity more in theory than in practice. The prevalence of interethnic violence and the abuse of women by men is surely related to brute differences between the groups in question. Yet the differences among humans seem slight compared with differences between humans and chimpanzees, gorillas, or orangutans. The idea of admitting our moral equality with such creatures seems outlandish in the face of such differences.

However, it is interesting to note that perception of difference often shifts

once moral equality is recognized. Before emancipation (and still among some confirmed racists), American blacks were often perceived as more like apes or monkeys than like Caucasian humans. Once moral equality was admitted, perceptions of identity and difference began to change. Increasingly blacks came to be viewed as part of the "human family", all of whose members are regarded as qualitatively different from "mere animals". Perhaps some day we will reach a stage in which the similarities among the great apes will be salient for us, and the differences among them will be dismissed as trivial and unimportant, or perhaps even enriching.

A third source of human resistance to equality for great apes is the lack of voices calling for such equality. The recognition of equality is deeply affected by empathy and sympathetic identification. It is difficult to identify or empathize with creatures who are remote, and whose plight is not directly articulated. Indeed the psychological importance of nearness is part of the reason why the plight of African humans is so often overlooked. Many Africans currently face famine, yet the industrialized would seems much more concerned with the less serious plights of its own victims of recession.

Even when the oppressed or disadvantaged have powerful and articulate champions, the victims themselves are often much more effective than their advocates. This aspect of human psychology has been repeatedly exploited by promoters of animal research whose public relations campaigns often feature children who claim to be alive and happy because of experimentation on animals. These individuals, victims of disease or disability, are often more effective advocates for research than scientists. The problem with the other great apes, however, is that they are not in a position to communicate effectively with humans. As a result their case must be made by humans, and such appeals have limited efficacy.

A fourth source of the human resistance to equality is that recognition of the setback to human interests that would result. The broader the membership of the community of equals, the fewer the benefits that accrue to the members. This is part of the reason that there has been historical resistance to expanding the circle of moral concern. Societal elites have resisted claims of equality from the inferior classes; men have resisted such claims from women; and whites have resisted the claims put forward by blacks. The loss of unjust advantage is part of the cost of life in a morally well-ordered society, but those who stand to bear the cost typically try to evade it.

Perhaps the deepest source of human resistance is that claims of equality among the great apes involve a fundamental conflict with the inherited Middle Eastern cultural and religious worldview of most Western societies. Judaism, Christianity, and Islam all grant humans a special place in nature. In orthodox Christian views humans are so special that God even took the form of a human; it would be unthinkable that He would have taken the form of a chimpanzee, gorilla, or orangutan. Even unbelievers live with the legacy of these traditions. The specialness of humans in nature is part of the background of our belief and action. Yet, as James Rachels (1990) has

powerfully argued, this picture in which human uniqueness plays such an important role is being undermined by the emerging worldview of science and philosophy. A secular picture that takes evolutionary theory seriously provides no support for human privilege. On this view, humans are seen as one species among many, rather than one species over many; in the long run humans are destined to go the way of other extinct species, and there is nothing in the scientific picture that directly supports the idea that this would be a loss. Of course there is no direct logical contradiction between the scientific worldview and claims about human uniqueness: One can continue to hold both, as many people do. What the scientific worldview does, however, is to remove much of the background that once gave plausibility to claims about human uniqueness. Without this background, such claims increasingly seem ad hoc and unsupported.

In this chapter I have tried to identify some of the sources of human resistance to acknowledging the moral equality of the great apes. Seen from a certain perspective, what is surprising is not that a distinguished group of scientists and philosophers are willing to assert such equality, but rather that such claims seem absurd to so many people. What I have suggested is that this initial impression of absurdity may be an expression of deep-seated fears and anxieties about our place in nature and our relations with those who are different. Even if this diagnosis is correct, such fears and anxieties will not instantly disappear. We have a long way to go before our emerging naturalistic worldview will fully inform our relationship with the rest of the nature. But before our demons can be tamed they must be identified and understood. I have tried to take a first step towards such identification and understanding.[2]

NOTES

1 © Reprinted from *Morality's Progress* (2002), pp. 47–51, by Dale Jamieson by permission of Oxford University Press.
2 I am grateful to Paola Cavalieri, Peter Singer, and Richard Sorabji for their comments on earlier drafts of this chapter.

12 Apes and human dignity

Matthias Kettner

In his contribution to the present volume, Dale Jamieson (Chapter 11) identifies several sources of the human resistance to acknowledging the moral equality of the great apes. He identifies five such sources in terms of the reasons that people typically give against the claim that we should recognize "our moral equality with the other great apes". According to Jamieson's speculative diagnosis, such reasons typically concern (1) the menace of momentous practical implications ("radical social change", in Jamieson's words) that recognizing other great apes as our moral equals would probably bring; (2) massive differences in appearance between us and other apes that make the idea our moral equality with such creatures "seem outlandish"; (3) the inability of other apes to communicate effectively with humans, which means that humans must argue their case for them "and such appeals have limited efficacy"; (4) recognition of the setback to human interests that would result from removing the moral species barrier between us and other apes; and, finally, (5) the religious entrenchment of a strong moral barrier between human beings and other animals: "In orthodox Christian views humans are so special that God even took the form of a human; it would be unthinkable that He would have taken the form of a chimpanzee, gorilla, or orangutan" (p. 201).

In my view, Jamieson's analysis of the resistance to transhuman moral universalism contains important insights into the psychology of speciesism. However, his analysis presupposes that there are compelling reasons for thinking that the great apes really *are* our moral equals. I doubt that there are such reasons. I do not doubt that we have many good reasons for protecting the great apes because there are many aspects under which we can appreciate them as highly valuable creatures. For instance, we might admire orangutans for their strength; we might attribute personality and individual temperament to chimpanzees when we are in a position to get to know them, as for instance in field research; and we might develop protective attitudes towards apes once we recognize the plight of those who are used as laboratory animals under conditions that we find abhorrent. Rather, what I want to question is whether there are reasons available to anyone who is prepared to consider the matter seriously that would make it seem similarly morally unavoidable to

include all great apes in the scope of our most important universalistic moral claims, as it indeed seems morally unavoidable to include all human beings in the scope of our most important universalistic moral claims. After all, Jamieson's analysis is not an analysis of resistance to the inclusion of apes into *any* kind of human moral concern. Jamieson analyses specifically the sources of resistance to construing apes and us as moral peers. Among us humans as moral peers, the most important universalistic moral claims pertain to basic rights, and correspondingly, to human dignity as underwriting human rights.

Consider the following. Our notion of human rights specifies our more general normative notion that there can be rights that every being of a certain kind has categorically and that every being of that kind has a fundamental duty to respect. In today's moral and political vocabulary, to speak of human rights is to speak of basic moral guarantees that all people have simply as people. Saying that human rights are *rights* suggests that they are high priority norms—"trumps" in Ronald Dworkin's (1977) metaphorical phrase—and that compliance with them is mandatory rather than discretionary. To say that the possessors of human rights are *all people simply as people* is, of course, nothing but a politically convenient way of bypassing the philosophically intriguing question of how to characterize the possessors of human rights so as to illuminate the features that are relevant, necessary, or even sufficient for making them such possessors. The Great Ape Project, which has developed since 1993 from Peter Singer's campaign for animal liberation, has as its central aim the inclusion of chimpanzees, gorillas, and orangutans in the same moral community that renders all people simply as people bearers of human rights. The Declaration on Great Apes, a moral-legal document modelled on the declaration of human rights, demands

> the extension of the community of equals to include all great apes: human beings, chimpanzees, gorillas and orangutans. "The community of equals" is the moral community within which we accept certain basic moral principles or rights as governing our relations with each other and enforceable at law.
>
> (Cavalieri & Singer, 1993, p. 4)

Among these, according to the Declaration on Great Apes, are the right to life, the protection of individual liberty, and the prohibition of torture.

In the next section I argue that human rights are a species-specific expression of human dignity. Human dignity is a notion that does not necessarily preclude nonhuman beings from possessing an equivalent of human dignity. Next, I argue that the extension of the notion of human dignity is not fixed by biology. Human dignity does not pertain to human beings qua members of a biological kind but qua members of a kind that is such that its members normally develop a moral stance (section 2). Finally, I conclude that we have no reason to extend the community of bearers of human dignity to other

kinds of great apes because no other kind of great apes, as far as we know, is such that its members normally develop a moral stance.

HAVING DIGNITY

The term "human rights" contains a natural-kind term. But if Hume's dictum that no *ought* derives from *is* alone holds, as I think it does, then merely from the fact that *x* is of kind K, where K is a natural kind, we cannot derive any normative conclusion, let alone categorical rights, on pain of begging the question. Historically, those language games in which the concept of human rights has been formed have built generality, egalitarianism, and a species-specific constraint into the very idea of human rights. Such rights hold equally and generally for human beings and not for nonhuman beings. As a matter of fact, we do not recognize any "bovine rights", "octopus rights", "seaweed rights", or, for that matter, "other great apes rights". Jamieson and other advocates of the Great Ape Project think that we ought to despecify our present practice of ascribing human rights. As they see it, the species-specific constraint on our present practice is based on speciesist and narcissistic reasons alone, i.e., we reap potential benefits of such rights for *people like us* and we disregard the fact that by doing so we discriminate against *beings similar to us*, at least in the case of other great apes.

It is true that if our practice of species-specific basic rights ascriptions were merely grounded on biological descriptions of people like us, or merely rooted in the historical contingency of our relevant vocabulary, such ascriptions would not be properly grounded at all. In order to be properly grounded, our practice of species-specific basic rights ascriptions must be underwritten by some suitable normative content that is already built into the specification of the kind in question. What kind of normative content might that be?

Here are the beginnings of a plausible answer. Basic rights pertain to members of a certain kind in virtue of the dignity that pertains to members qua members of that kind. To have dignity qua membership is a categorical relation; to possess certain rights pertaining to that dignity is a categoric relation; hence, being a member of the appropriate kind and by transitivity possessing certain rights are categorically conjoined, even though they are not conceptually identical.

How can dignity give rise to rights? Dignity is a concept with a complex history. However, a simple, but powerful, intuition gives the notion of dignity its rights-generating normative power. The core intuition as to what it means *for a specimen x of kind X to have dignity* can be expressed as follows:

(D)   For *x* to have dignity is

    1 to be recognized by others
    2 as commanding their respect
    3 in ways that are appropriate to the dignity they know *X* to have.

Let me elaborate. (D) is not an attempt to give necessary and sufficient conditions for the meaning of "dignity". (D) articulates the conceptual structure of *having* dignity. That the term "dignity" appears in the definiens is not an indication of vicious circularity; rather, it registers the fact that the notion of dignity contains two complementary perspectives: the self-regarding perspective of the manifester of dignity, and the other-regarding perspective of whoever recognizes the manifester of dignity as having dignity. Dignity is the intentional object of the respect, i.e., that which is being respected. Respecting dignity requires qualified ways of treating and appreciating the manifester of dignity, namely ways that are oriented by the determinate dignity that figures as the intentional object of such respect. The recognition that goes with *x*'s having dignity is the recognition that *x* manifests the dignity of kind *X*. So far so good. But a crucial question remains. How can *x*'s being recognized by *y* and *z* as manifesting the dignity of kind *X* prescribe and proscribe anything to *y* and *z*?

Note that (D) indicates where a suitable normative content must be conceptually located—namely in the specification of the kind in question, *X*, but (D) does not yet provide that content. No natural kind term will do for *X* on pain of a naturalistic fallacy. Nor will a kind term of a purely normative nature, e.g., "rational being", do the job that *X* does in (D). *X* must contain enough descriptive content to help us decide whether some given *x* is in fact a particular instance of the kind *X*. This is where many criticisms of the alleged speciesism in human rights and human dignity discourse go wrong. Because they fail to distinguish the reasons we use for judging something to be an instance of *X*, and the reasons we use for judging behaviour involving instances of *X* as proper or improper, they think that basing human dignity and human rights on membership to kind *X* (where *X* picks out the species *Homo sapiens*) is sucking normative honey out of descriptive criteria, i.e., a naturalistic fallacy. For instance, failing to distinguish the descriptions that biologists and anthropologists use for judging a particular living organism to be a human being from the reasons we have for judging that human beings have human dignity and therefore possess an inalienable right not to be subjected to torture, makes it seem as if we were transfiguring our common biological nature into something of supreme normative importance. However, this impression of a naturalistic fallacy in favour of our biological species is a false impression. We see this clearly once we analytically separate criteria for the *ascription* of human dignity and human rights from reasons for *justifying*

whatever normative implications we take our notions of human dignity and human rights to have.

HUMAN DIGNITY AS THE MORAL STATUS OF GIVERS OF MORAL STATUS

Note also that nothing in the analysis (D) so far rules out the possibility of different normative kinds giving rise to different notions of dignity. (D) is compatible with our possible recognition of, e.g., bovine dignity B, or chimpanzee dignity C. Such dignity would prescribe and proscribe certain ways of treating cows, or chimps, as giving proper expression to respect for bovine dignity and chimpanzee dignity, respectively. And the corresponding norms, e.g., rights-claims, that would codify proper ways of treating cows, or chimps, could differ characteristically from the norms that qualify ways of treating human beings as giving proper expression to respect for human dignity H. To say that the relation of having dignity is amenable to a pluralistic interpretation is not the same, of course, as saying that any one type of dignity can be extended so as to cover the extension of any other type of dignity. Assume that we can make sense not only of H, as we certainly can, but also of B and C. It follows neither that we can make sense of running together H and C, or B, nor that H could be broadened so as to subsume C, or B. But can we indeed make sense of C?

Earlier I argued that we can respond to the crucial question of how x's being recognized by y and z as manifesting the dignity of X can prescribe and proscribe anything at all to y and z by articulating our reasons for justifying the normative implications with which we use such concepts as human dignity and human rights. At this point, Jamieson along with other advocates of the Declaration on Great Apes wants to argue that once we articulate our reasons for justifying the familiar normative implications of human dignity, e.g., basic rights to life, protection of individual liberty, and prohibition of torture, we are obligated to recognize that the same reasons commit us to extending the familiar normative implications of dignity for humans to other great apes as well. Jamieson's chapter is an attempt to draw attention to the psychological factors that would make it hard for us to fully realize and bear out this commitment.

I doubt that we are so committed. In order to see that we are not, consider the following reason for giving the concept H its familiar normative implications. In virtue of being human, we all belong to a kind of which it is characteristic that its members consider it natural for all members to develop some moral stance or other in the course of their personal life. (There are, of course, many other things that are characteristic of human beings. For instance, we consider it natural, or "normal", that human beings develop a personal identity, learn to speak a language, acquire sexual preferences, etc.) No matter what particular moral stance people develop and no matter

whether different moral stances conflict, by developing any moral stance at all one will manifest oneself as both a source of moral concerns for others and as an object of others' moral concerns. Such concerns may differ wildly. The object range of our moral concerns is extremely flexible. We can recognize moral status in wild orchids and we can give different moral status to sentient beings, higher animals, and our human peers. In all this we manifest ourselves as givers of moral status. Our own moral status is the status of being able to confer (all kinds of) moral status, including our own. This asymmetry sets us over and against anything on which we confer moral status, which does not confer moral status on us in return. It is this asymmetry that we acknowledge when we recognize ourselves and human beings in general as commanding our respect in ways that are appropriate to being typically both a source and an object of moral concerns.

THE STATUS DIFFERENCE BETWEEN NONHUMAN GREAT APES AND US

In the previous section, the notion of human dignity turned out to be a particular moral status within a number of actual and possible moral statuses. Thinking about human beings in terms of human dignity is thinking about human beings in their capacity as moral status givers with regard to each other and to nonhuman beings. If this analysis is sound, we would have a compelling reason to extend the community of bearers of human dignity to other kinds of great apes, if it were a fact that members of other kinds of great apes normally develop a moral stance.

There is ample evidence that other great apes are capable of a surprising variety of things that we once proudly thought only humans could do. The scope of great ape intelligence is a case in point. Typically, great apes can console, imitate, pretend, fool, use tools, and exhibit a sense of self. However, if nonhuman great apes typically follow moral rules and develop moral concerns, it is a secret that great ape researchers have kept very well. Learning to give moral status to members of a certain kind and elaborating we-intentions of the form that everyone impartially wants everyone else to want to behave in certain ways are activities that require capacities well beyond altruistic attitudes, imitation, and punishing and reward patterns that constitute the somewhat inchoate protomorality of which great apes are demonstrably capable. The beginnings and precursors of morality do not amount to morality as we know it. On the contrary, human dignity is a symbolic expression of the root of morality as we know it. As long as there is no evidence that apes and human beings can enter on an equal footing into *our* community of moral communication, attributions of counterparts of human dignity and human rights to other great apes have nothing to latch onto. Human dignity is not on a par with other forms of species-specific dignity. Rather, human dignity is (nonmetaphysically) necessary for all other forms of moral status to be possible.

Postscript

Human uniqueness in a comparative perspective

Louise S. Röska-Hardy

The views presented in this volume are as diverse as the theoretical and methodological approaches pursued in comparative studies. Nevertheless, each provides insights into potential commonalities between nonhuman animals and humans as well as clues to crucial differences. Some contributors explore possible evolutionary continuities and their implications; others argue that distinctive human capacities developed along a unique evolutionary path. Despite different views on questions of continuity versus discontinuity, all assume that there is an evolutionary story to be told, i.e., they agree that humans' capacities are the result of diverse evolutionary processes. In adopting a comparative perspective in their work, they seek to place species-specific capacities—both human and nonhuman—in an evolutionary context. This is an important step towards understanding human uniqueness.

First of all, from an evolutionary standpoint all species are unique in possessing traits that other species do not. We humans are not unique in being unique. Importantly, in order to determine which capacities are uniquely human, we need to know which capacities other animals possess. Comparative studies offer a valuable approach to identifying the behavioural and cognitive capacities that humans share with other animals as well as those that are specifically human. Thus, they provide a starting point for examining the uniqueness of human traits within an evolutionary perspective.

Second, even though the claim that a particular capacity is uniquely human may strike us as obviously true, empirical evidence is needed to substantiate the claim. For reasons of inductive logic, empirical findings cannot conclusively establish a claim to uniqueness. However, the hypothesis can be indirectly substantiated by investigating the abilities of nonhuman animals. If it can be shown that other animals do not possess the capacity in question, the claim to uniqueness is strengthened. The experimental data generated in comparative studies play a crucial role here; several abilities once thought to be uniquely human have been shown to exist in nonhuman animals.

Third, for the interdisciplinary analysis of evolutionary patterns, the crucial question is not whether human-specific capacities resemble or differ from those of other animals, but how and in what respect they do so. It is a matter of discerning the *nature* of human uniqueness. Here, too, comparative

studies can contribute. A full account of human uniqueness will go beyond cataloguing the similarities and differences between humans and non-human animals to suggest hypotheses about evolutionary paths. It will situate conjectures about the development of human language, cognition, and culture within an evolutionary framework. This goal does not preclude the discovery of fundamental differences between humans and nonhuman animals. On the contrary, to the extent that particular capacities are distinctly hominid, no counterparts in nonhuman animals are to be expected. Rather, the idea is that understanding the nature of human uniqueness involves assessing the differences between humans and other animals in the light of commonalities. This in turn will provide a basis for considering whether humans are "uniquely unique" in the sense that their species-specific capacities combined to produce a set of evolutionarily new paths, e.g., channels of nongenetic inheritance.

Fundamental questions about the nature and provenance of modern humans' capacities are unlikely to be resolved by any single discipline. Achieving an understanding of human language, cognition, and culture and their place in nature will require a collaborative, multidisciplinary effort. The apparent discontinuity of human capacities from everything else to be found in nature makes the task daunting. However, if comparative studies allow us to identify and to study examples of homology and analogy, we can begin to address questions about the origins, selective pressures, and evolutionary trajectories of specifically human traits. In this way, comparative studies of nonhuman animals may provide us with a clearer perspective on the nature of human uniqueness. They may help us discover what makes us unique relative to other animals and permit inferences concerning the evolutionary origins of our remarkable capacities. In sum, there is much to learn from animals about what makes us uniquely human.

References

Adamson, L. (1996). *Communication development during infancy*. Oxford, UK: Westview.

Adamson, L. B., & Bakeman, R. (1991). The development of shared attention during infancy. In R. Vasta (Ed.), *Annals of child development* (Vol. 8, pp. 1–41). London: Jessica Kingsley Publishers.

Aitken, P. G. (1981). Cortical control of conditioned and spontaneous vocal behavior in rhesus monkeys. *Brain and Language*, *13*, 171–184.

Akins, C. K., & Zentall, T. R. (1998). Imitation in Japanese quail: The role of reinforcement of demonstrator responding. *Psychonomic Bulletin and Review*, *5*, 694–697.

Alberts, S. C. (1994). Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. *Animal Behaviour*, *47*, 749–755.

Allan, K. (2007). "General" or "universal" grammar: from the modistae to Chomsky. In K. Allan (Ed.), *The Western classical tradition in linguistics* (pp. 153–187). London/Oakville: Equinox.

Allen-Hermanson, S. (2005). Morgan's canon revisited. *Philosophy of Science*, *72*, 608–631.

Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*, *37*, 47–55.

Anderson, J. R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, *49*, 201–208.

Annett, M. (1985). *Left, right, hand and brain: The right shift theory*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Anscombe, G. E. M. (1957). *Intention*. Oxford, UK: Basil Blackwell.

Arbib, M. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences*, *28*, 105–167.

Arbib, M. (Ed.). (2006). *Action to language via the mirror neuron system*. Cambridge, UK: Cambridge University Press.

Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. *American Journal of Primatology*, *39*, 159–178.

Aristotle (350 BC). *The history of animals*. London: Heinemann.

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, *441*, 303.

Aureli, F., & Schaffner, C. M. (2006). Causes, consequences and mechanisms of reconciliation: The role of cooperation. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 121–136). Heidelberg, Germany Springer.

Austin, P., & Bresnan, J. (1996). Non-configurationality in Australian aboriginal languages. *Natural Language and Linguistic Theory*, *14*, 215–268.

Autumn, K., Ryan, M. J., & Wake, D. B. (2002). Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology*, *77*, 383–408.

Bales, K., Dietz, J., Baker, A., Miller, K., & Tardif, S. D. (2000). Effects of allocaregivers on fitness of infants and parents in callitrichid primates. *Folia Primatology*, *71*, 27–38.

Ballard, D. (1999). *An introduction to natural computation*. Cambridge, MA: MIT Press.

Bard, K. A. (1990). "Social tool use" by free-ranging orangutans: A Piagetian and developmental perspective on the manipulation of an animate object. In S. T. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 356–378). New York: Cambridge University Press.

Bard, K. A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development*, *63*, 1186–1197.

Bard, K. A. (1994). Evolutionary roots of intuitive parenting: Maternal competence in chimpanzees. *Early Development and Parenting*, *3*, 19–28.

Bard, K. A. (1996). *Responsive care: A behavioral intervention program for nursery-reared chimpanzees*. Tuscon, AZ: Jane Goodall Institute.

Bard, K. A. (2000). Crying in infant primates: Insights into the development of crying in chimpanzees. In R. G. Barr, B. Hopkins, & J. A. Green (Eds.), *Crying as a sign, a symptom, and a signal: Clinical emotional and developmental aspects of infant and toddler crying* (pp. 157–175). New York: Cambridge University Press.

Bard, K. A. (2005). Emotions in chimpanzee infants: The value of a comparative developmental approach to understand the evolutionary bases of emotion. In J. Nadel & D. Muir (Eds.), *Emotional development: Recent research advances* (pp. 31–60). New York: Oxford University Press.

Bard, K. A. (2007). Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Animal Cognition*, *10*, 233–242.

Bard, K. A., Bulbrook, S., Maguire, V., Veira, Y., Hayes, K., & McDonald, K. (under review). Developmental milestones in social skills and social "manners" of young chimpanzees.

Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees: Enculturation, temperament, and cognition. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 235–256). New York: Cambridge University Press.

Bard, K. A., Hopkins, W. D., & Fort, C. (1990). Lateral bias in infant chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *104*, 309–321.

Bard, K. A., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Costall, A., & Matsuzawa, T. (2005). Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology*, *41*, 616–624.

Bard, K. A., Platzman, K. A., Lester, B. M., & Suomi, S. J. (1992). Orientation to social and nonsocial stimuli in neonatal chimpanzees and humans. *Infant Behavior and Development*, *15*, 43–56.

Bard, K. A., Platzman, K. A., Lester, B. M., & Suomi, S. J. (2001). Développement neurobiologique et émotions chez les nouveau-nés chimpanzés et humains [Neuro-behavioral integrity and emotions in chimpanzee and human neonates]. *Enfance*, *3*, 226–235.

Bard, K. A., & Russell, C. L. (1999). Evolutionary foundations of imitation: Social, cognitive, and developmental aspects of imitative processes in non-human primates. In J. Nadel & G. Butterworth (Eds.), *Imitation in infancy* (pp. 89–123). New York: Cambridge University Press.

Bard, K. A., Todd, B. K., Bernier, C., Love, J., & Leavens, D. A. (2006). Self-awareness in human and chimpanzee infants: What is measured and what is meant by the mark and mirror test? *Infancy*, *9*, 191–219.

Bard, K. A., & Vauclair, J. (1984). The communicative context of manipulation in ape and human adult–infant pairs. *Journal of Human Evolution*, *13*, 181–190.

Baron-Cohen, S. (1999). The evolution of a theory of mind. In M. C. Corballis & S. E. G. Lea (Eds.), *The descent of mind: Psychological perspectives on hominid evolution* (pp. 261–277). Oxford, UK: Oxford University Press.

Baron-Cohen, S., Tager-Flusberg, H., & Cohen, D. J. (2000). *Understanding other minds: Perspectives from developmental cognitive neuroscience* (2nd ed.). Oxford, UK: Oxford University Press.

Bartlett, F. C. (1932). *Remembering*. Cambridge, UK: Cambridge University Press.

Bates, E. (1976). *Language and context: The acquisition of pragmatics*. New York: Academic Press.

Bates, E., O'Connell, B., & Shore, C. (1987). Language and communication in infancy. In J. Osofsky (Ed.), *Handbook of infant development* (2nd ed., pp. 149–203). New York: Wiley.

Baum, W. M., Richerson, P. J., Efferson, C. M., & Paciotti, B. M. (2004). Cultural evolution in laboratory microsocieties including traditions of rule giving and rule following. *Evolution and Human Behavior*, *25*, 305–326.

Bayley, N. (1969). *Bayley scales of infant development*. New York: Psychological Corporation.

Behne, T., Carpenter, M., Call, J., & Tomasello, M. (2005). Unwilling versus unable: Infants' understanding of intentional action. *Developmental Psychology*, *41*, 328–337.

Bennett, J. (1978). Some remarks about concepts. *Behavioral and Brain Sciences*, *4*, 557–560.

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science*, *302*, 1234–1236.

Bermudez, J. (2003). *Thinking without words*. Oxford, UK: Oxford University Press.

Bernardis, P., & Gentilucci, M. (2006). Speech and gesture share the same communication system. *Neuropsychologia*, *44*, 178–190.

Bethell, E., Vick, S.-J., & Bard, K. A. (2007). Measurement of eye gaze in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *69*, 562–575.

Bickerton, D. (1990). *Language and species*. Chicago: Chicago University Press.

Bickerton, D. (1995). *Language and human behavior*. Seattle, WA: University of Washington Press.

Blake, J., O'Rourke, P., & Borzellino, G. (1994). Form and function in the development of pointing and reaching gestures. *Infant Behavior and Development*, *17*, 195–203.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*, 530–532.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, *12*, 82–91.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai-National-Park. *American Journal of Physical Anthropology*, *78*, 547–573.

Boitani, L., & Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. *Ethology, Ecology and Evolution*, *7*, 49–72.

Bolhuis, J. J., & Macphail, E. M. (2001). A critique of the neuroecology of learning and memory. *Trends in Cognitive Science*, *5*, 426–433.

Bonvillian, J. D., Richards, H. C., & Dooley, T. T. (1997). Early sign language acquisition and the development of hand preferences in young children. *Brain and Language*, *58*, 1–22.

Borofsky, R., Barth, F., Shweder, R. A., Rodseth L., & Stolzenberg, N. M. (2001). WHEN: A conversation about culture. *American Anthropologist*, *103*, 432–446.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: Chicago University Press.

Boyd, R., & Richerson, P. J. (2005). *The origin and evolution of cultures*. Oxford, UK: Oxford University Press.

Böye, M., Guntürkün, O., & Vauclair, J. (2005). Right ear advantage for conspecific calls in adults and subadults, but not infants, California sea lions (*Zalophus californianus*): Hemispheric specialization for communication? *European Journal of Neuroscience*, *21*, 1727–1732.

Bradshaw, J. L., & Rogers, L. (1993). *The evolution of lateral asymmetries, language, tool-use and intellect*. San Diego, CA: Academic Press.

Bratman, M. (1992). Shared cooperative activity. *Philosophical Review*, *101*, 327–341.

Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, *119*, 145–154.

Brentano, F. (1973). *Psychologie vom empirischen Standpunkt* [*Psychology from an empirical standpoint*]. Hamburg, Germany: Meiner. (Original work published 1874)

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology*, *3*, e380.

Briscoe, E. J. (2003). Grammatical assimilation. In M. H. Christiansen & S. Kirby (Eds.), *Language evolution: The states of the art* (pp. 295–316). Oxford, UK: Oxford University Press.

Broca, P. (1865). Sur le siège de la faculté du langage articulé [Remarks on the seat of the faculty of articulate language]. *Bulletins de la Société d'Anthropologie de Paris*, *6*, 377–393.

Brockelman, W. Y., & Schilling, D. (1984). Inheritance of stereotyped gibbon calls. *Nature*, *312*, 634–636.

Brown, D. E. (1991). *Human universals*. New York: McGraw-Hill.

Brown, G. R., Almond, R. E. A., & van Bergen, Y. (2004). Begging, stealing and offering: Food transfer in nonhuman primates. *Advances in the Study of Behaviour*, *34*, 265–295.

Brownell, C., & Carriger, M. S. (1990). Changes in cooperation and self-other differentiation during the second year. *Child Development*, *61*, 1164–1174.

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: Regulation of call characteristics in a New World monkey. *Journal of Experimental Biology*, *207*, 443–448.

Bruner, J. (1995). From joint attention to the meeting of minds: An introduction. In

C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 1–14). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour*, *54*, 817–831.

Bullowa, M. (Ed.). (1979). *Before speech: The beginnings of interpersonal communication*. New York: Cambridge University Press.

Burkart, J. M., & Heschl, A. (2006). Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, *120*, 120–130.

Burkart, J. M., & Heschl, A. (2007). Perspective taking or behaviour reading? Understanding of visual access in common marmosets (*Calithrix jacchus*). *Animal Behaviour*, *73*, 457–469.

Byrne, R. W. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford, UK: University Press.

Byrne, R. W., Barnard, P. J., Davidson, I., Janik, V. M., McGrew, W. C., Miklósi, Á., & Wiessner, P. (2004). Understanding culture across species. *Trends in Cognitive Sciences*, *8*, 341–346.

Byrne, R. W., & Whiten, A. (Eds.). (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford, UK: Oxford University Press.

Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, *50*, 53–60.

Caldwell, C., & Whiten, A. (2002). Evolutionary perspectives on imitation: Is a comparative psychology of social learning possible? *Animal Cognition*, *5*, 193–208.

Caldwell, C. A., & Whiten, A. (2004). Testing for social learning and imitation in common marmosets, *Callithrix jacchus*, using an artificial fruit. *Animal Cognition*, *7*, 77–85.

Caldwell, C. A., & Whiten, A. (2006). Social learning in monkeys and apes: Cultural animals? In C. J. C. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 652–664). Oxford, UK: Oxford University Press.

Call, J., Agnetta, B., & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, *3*, 23–34.

Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 211–228). Cambridge, MA: MIT Press.

Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). "Unwilling" versus "unable": Chimpanzees' understanding of human intentional action. *Developmental Science*, *7*, 488–498.

Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, *108*, 307–317.

Call, J., & Tomasello, M. (1996). The effect of humans on cognitive development of apes. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371–403). New York: Cambridge University Press.

Call, J., & Tomasello, M. (1999). A nonverbal false belief task: The performance of children and great apes. *Child Development*, *70*, 381–395.

Calvin, W. H. (1983). A stone's throw and its launch window: Timing precision and its implications for language and hominid brains. *Journal of Theoretical Biology*, *104*, 121–135.

Campbell, A. L., & Namy, L. L. (2003). The role of social referential cues in verbal and non-verbal symbol learning. *Child Development*, *74*, 549–563.

Camper, P. (1779). Account of the organs of speech of the orang outang. *Philosophical Transactions of the Royal Society of London*, *69*, 139–159.

Cantalupo, C., & Hopkins, W. D. (2001). Asymmetrical Broca's area in great apes. *Nature*, *414*, 505.

Caplan, D. (1987). *Neurolinguistics and linguistic aphasiology*. New York: McGraw-Hill.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology*, *67*, 151–174.

Carpendale, J., & Lewis, C. (2006). *How children develop social understanding*. Oxford, UK: Blackwell.

Carpenter, M., Nagell, K., & Tomasello, M. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the Society for Research in Child Development*, *63*, 176.

Carpenter, M., Tomasello, M., & Savage-Rumbaugh, S. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, *4*, 217–237.

Carpenter, M., Tomasello, M., & Striano, T. (2005). Role reversal imitation and language in typically developing infants and children with autism. *Infancy*, *8*, 253–278.

Carroll, S. B. (2003). Genetics and the making of *Homo sapiens. Nature*, *422*, 849–857.

Carroll, S. B. (2005). *Endless forms most beautiful*. New York: W. W. Norton.

Carroll, S. B., Grenier, J. K., & Weatherbee, S. D. (2005). *From DNA to diversity: Molecular genetics and the evolution of animal design*. Malden, MA: Blackwell Science.

Casler, K., & Kelemen, D. (2005). Young children's rapid learning about artifact functions. *Developmental Science*, *8*, 472–480.

Catchpole, C. K. (1973). The functions of advertising song in the sedge warbler (*Acrocephalus schoenobaenus*) and reed warbler (*A. scirpaceus*). *Behaviour*, *46*, 300–320.

Catchpole, C. K., & Slater, P. L. B. (1995). *Bird song: Themes and variations*. New York: Cambridge University Press.

Cavalieri, P., & Singer, P. (1993). *The great ape project: Equality beyond humanity*. London: Fourth Estate.

Chappell, J., & Kacelnik, A. (2002). Tool-selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, *5*, 71–78.

Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, *28*, 362–367.

Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, *36*, 477–486.

Cheney, D. L., & Seyfarth, R. M. (1990a). Attending to behaviour versus attending to knowledge: Examining monkey's attribution of mental states. *Animal Behaviour*, *40*, 742–753.

Cheney, D. L., & Seyfarth, R. M. (1990b). *How monkeys see the world*. Chicago: University of Chicago Press.

Cheney, D. L., & Seyfarth, R. M. (1990c). The representation of social relations by monkeys. *Cognition*, *37*, 167–196.

Cheney, D. L., & Seyfarth, R. M. (1999). Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*, *58*, 67–75.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The responses of female baboons

(*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? *Journal of Comparative Psychology*, *109*, 134–141.

Chisholm, J. S. (2003). Uncertainty, contingency, and attachment: A life history theory of theory of mind. In K. Sterelny & J. Fitness (Eds.), *From mating to mentality: Evaluating evolutionary psychology* (pp. 125–154). New York: Psychology Press.

Chomsky, N. (1965). *Aspects of the theory of syntax*. Cambridge, MA: MIT Press.

Chomsky, N. (1966). *Cartesian linguistics: A chapter in the history of rationalist thought*. New York: Harper & Row.

Chomsky, N. (1988). *Language and the problems of knowledge: The Managua lectures*. Cambridge, MA: MIT Press.

Chomsky, N. (1995). Bare phrase structure. In G. Webelknuth (Ed.), *Government and binding theory and the minimalist program* (pp. 383–439). Cambridge, MA: Blackwell.

Chomsky, N. (2005). Three factors in language design. *Linguistic Inquiry*, *36*, 1–22.

Christiansen, M. H., & Kirby, S. (2003). Language evolution: Consensus and controversies. *Trends in Cognitive Sciences*, *7*, 300–307.

Clark, A. (1997). *Being there: Putting brain, body and world together again*. Cambridge, MA: MIT Press.

Clark, A., & Chalmers, D. (1998). The extended mind. *Analysis*, *58*, 7–19.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PLoS ONE*, *1*, e73.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, *4*, 685–691.

Cohen, L. B. (1972). Attention-getting and attention-holding processes of infant visual preferences. *Child Development*, *43*, 869–879.

Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.

Corballis, M. C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences*, *26*, 199–260.

Corina, D. P., Vaid, J., & Bellugi, U. (1992). The linguistic basis for left hemisphere specialization. *Science*, *255*, 1258–1260.

Corson, S. A., Corson, E. O'L., Becker, R. E., Ginsburg, B. E., Trattner, A., Connor, R. L., et al. (1980). Interaction of genetics and separation in canine hyperkinesis and in differential responses to amphetamine. *Pavlovian Journal of Biological Sciences*, *15*, 5–11.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*, 1441–1453.

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology*, *110*, 221–243.

Cronin, K. A., Kurian, A. V., & Snowdon, C. T. (2005). Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour*, *69*, 133–142.

Csibra, G. (2007). Teachers in the wild. *Trends in Cognitive Sciences*, *11*, 95–96.

Curio, E., Ernst, U., & Vieth, W. (1978). The adaptive significance of avian mobbing II—Cultural transmission of enemy recognition in blackbirds: Effectiveness and some constraints. *Zeitschrift fur Tierpsychologie*, *48*, 184–202.

Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit

task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *113*, 13–23.

Custance, D. M., Whiten, A., Sambrook, T., & Galdikas, B. (2001). Testing for social learning in the "artificial fruit" processing of wildborn orangutans (*Pongo pygmaeus*), Tanjung Puting, Indonesia. *Animal Cognition*, *4*, 305–313.

Cutler, A. (1996). Prosody and the word boundary problem. In J. L. Morgan & K. Demuth (Eds.), *Signal to syntax: Bootstrapping from speech to syntax in early acquisition* (pp. 87–100). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: John Murray.

Darwin, C. (1936a). *On the origin of species by means of natural selection*. New York: Random House. (Original work published 1859)

Darwin, C. (1936b). *The descent of man and selection in relation to sex*. New York: Random House. (Original work published 1871)

Dautenhahn, K., & Nehaniv, C. L. (2002). *Imitation in animals and artifacts*. Cambridge, MA: MIT Press.

Davidson, D. (1963). Actions, reasons and causes. *Journal of Philosophy*, *60*, 685–700.

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour*, *13*, 470–474.

De Condillac, E. B. (1947). *Oeuvres philosophiques de Condillac: Vol. 1. Essai sur l'origine des connaissances humaines* [*Essay on the origins of human knowledge*] (Georges LeRoy, Ed.). Paris: Presses Universitaires de France. (Original work published 1746)

Deacon, T. W. (1997). *The symbolic species: The co-evolution of language and the brain*. New York: Norton.

Deaner, R. O., van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology: Human-Nature.com/ep*, *4*, 149–196.

DeCasper, A. J., & Fifer, W. P. (1980). Of human bonding: Newborns prefer their mothers' voices. *Science*, *208*, 1174–1176.

Dennett, D. (1978). Beliefs about beliefs. *Behavioral and Brain Sciences*, *4*, 568–570.

Dennett, D. (1987). *The intentional stance*. Cambridge, MA: MIT Press.

Dennett, D., & Haugeland, J. (1987). Intentionality. In R. L. Gregory (Ed.), *The Oxford companion to the mind* (pp. 383–386). Oxford, UK: Oxford University Press.

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour*, *106*, 183–251.

de Waal, F. B. M. (2001). *The ape and the Sushi master: Cultural reflections of a primatologist*. New York: Basic Books.

De Wandelaer, T., & Burkart, J. M. (2008). Is there a relationship between gazing behaviour and social structure? An experimental study with common marmosets (*Callithrix jacchus*). *Manuscript in preparation*.

Dewson, J. H. (1977). Preliminary evidence of hemispheric asymmetry of auditory function in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 63–71). New York: Academic Press.

Digby, L. J. (1994). Social organization in a wild population of *Callithrix jacchus*: II. Intragroup social behavior. *Primates*, *36*, 361–375.

Dittus, W. (1984). Toque macaque food calls: Semantic communication concerning food distribution in the environment. *Animal Behaviour*, *32*, 470–477.

Donald, M. (1991). *Origins of the modern mind*. Cambridge, MA: Harvard University Press.

Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience*, *22*, 567–631.

Duncker, K. (1945). On problem solving. *Psychological Monographs*, *58*(5, Serial No. 270).

Dworkin, R. (1977). *Taking rights seriously*. Cambridge, MA: Harvard University Press.

Eckerman, C. O., & Didow, S. M. (1996). Nonverbal imitation and toddlers' mastery of verbal means of achieving coordinated action. *Developmental Psychology*, *32*, 141–152.

Ehert, G. (1987). Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature*, *325*, 249–251.

Ehrlich, P. (2002). *Human natures: Genes, cultures and the human prospect*. Washington, DC: Shearwater Books/Island Press.

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contributions to Zoology*, *213*, 1–108.

El'Konin, D. B. (1966). Symbolics and its function in the play of children. *Soviet Education*, *8*, 35–41.

Elder, J., & Pederson, D. (1978). Preschool children's use of objects in symbolic play. *Child Development*, *49*, 500–504.

Embick, D., & Poeppel, D. (2005). Mapping syntax using imaging: Prospects and problems for the study of neurolinguistic computation. In K. Brown (Ed.), *Encyclopedia of Language and Linguistics* (2nd ed., vol. 7, pp. 484–486). Oxford, UK: Elsevier.

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, *24*, 581–604.

Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., et al. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, *418*, 869–872.

Fauconnier, G. (1997). *Mappings in thought and language*. Cambridge, UK: Cambridge University Press.

Fauconnier, G., & Turner, M. (2002). *The way we think: Conceptual blending and the mind's hidden complexities*. New York: Basic Books.

Feistner, A. T., & Price, E. C. (1990). Food-sharing in cotton-top tamarins (*Saguinus Oedipus*). *Folia Primatologica*, *54*, 34–45.

Feistner, A. T., & Price, E. C. (1991). Food offering in New World primates: Two species added. *Folia Primatologica*, *57*, 165–168.

Feistner, A. T., & Price, E. C. (2000). Food sharing in black lion tamarins (*Leontopithecus crysopygus*). *American Journal of Primatology*, *52*, 47–54.

Feldman, N. W., & Laland, K. N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology and Evolution*, *11*, 453–457.

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience*, *17*, 1703–1714.

Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to the observation of actions made with tools in the monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, *17*, 212–226.

Ferrari, S. F. (1987). Food transfer in a wild marmoset group. *Folia Primatologica*, *48*, 203–206.

Fischer, A., Pollack, J., Thalmann, O., Nickel, B., & Pääbo, S. (2006). Demographic history and genetic differentiation in apes. *Current Biology*, *16*, 1133–1138.

Fischer, J. (2002). Developmental modifications in the vocal behavior of nonhuman primates. In A. A. Ghazanfar (Ed.), *Primate audition* (pp. 109–126). Boca Raton, FL: CRC Press.

Fischer, J., Hammerschmidt, K., & Todt, D. (1998). Local variation in Barbary macaque shrill barks. *Animal Behaviour*, *56*, 623–629.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*, 140–148.

Fitch, R. H., Brown, C. P., O'Connor, K., & Tallal, P. (1993). Function lateralization for auditory temporal processing in male and female rats. *Behavioral Neuroscience*, *107*, 844–850.

Fitch, W. T. (1994). *Vocal tract length perception and the evolution of language*. UMI Dissertation Services, Ann Arbor, MI.

Fitch, W. T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, *102*, 1213–1222.

Fitch, W. T. (1999). Acoustic exaggeration of size in birds by tracheal elongation: Comparative and theoretical analyses. *Journal of Zoology (London)*, *248*, 31–49.

Fitch, W. T. (2000a). Skull dimensions in relation to body size in nonhuman mammals: The causal bases for acoustic allometry. *Zoology*, *103*, 40–58.

Fitch, W. T. (2000b). The evolution of speech: A comparative review. *Trends in Cognitive Sciences*, *4*, 258–267.

Fitch, W. T. (2000c). The phonetic potential of nonhuman vocal tracts: Comparative cineradiographic observations of vocalizing animals. *Phonetica*, *57*, 205–218.

Fitch, W. T. (2002a). Comparative vocal production and the evolution of speech: Reinterpreting the descent of the larynx. In A. Wray (Ed.), *The transition to language* (pp. 21–45). Oxford, UK: Oxford University Press.

Fitch, W. T. (2002b). The evolution of language comes of age. *Trends in Cognitive Sciences*, *6*, 278–279.

Fitch, W. T. (2005a). Computation and cognition: Four distinctions and their implications. In A. Cutler (Ed.), *Twenty-first century psycholinguistics: Four cornerstones* (pp. 381–400). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Fitch, W. T. (2005b). The evolution of language: A comparative review. *Biology and Philosophy*, *20*, 193–230.

Fitch, W. T. (2006a). On the biology and evolution of music. *Music Perception*, 24, 85–88.

Fitch, W. T. (2006b). The biology and evolution of music: A comparative perspective. *Cognition*, *100*, 173–215.

Fitch, W. T. (2008). Nano-intentionality: In defense of intrinsic intentionality. *Biology and Philosophy*, *23*, 157–177.

Fitch, W. T. (in press). Three meanings of "recursion": Key distinctions for biolinguistics. In R. Larson, V. Deprez, & H. Yamakido (Eds.), *The evolution of human language: Biolinguistic perspectives*. Cambridge, UK: Cambridge University Press.

Fitch, W. T., & Fritz, J. B. (2006). Rhesus macaques spontaneously perceive formants

in conspecific vocalizations. *Journal of the Acoustical Society of America*, *120*, 2132–2141.

Fitch, W. T., & Giedd, J. (1999). Morphology and development of the human vocal tract: A study using magnetic resonance imaging. *Journal of the Acoustical Society of America*, *106*, 1511–1522.

Fitch, W. T., & Kelley, J. P. (2000). Perception of vocal tract resonances by whooping cranes, *Grus americana*. *Ethology*, *106*, 559–574.

Fitch, W. T., & Reby, D. (2001). The descended larynx is not uniquely human. *Proceedings of the Royal Society of London, Series B*, *268*, 1669–1675.

Fitch, W. T., & Hauser, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science*, *303*, 377–380.

Fitch, W. T., Hauser, M. D., & Chomsky, N. (2005). The evolution of the language faculty: Clarifications and implications. *Cognition*, *97*, 179–210.

Fivaz-Depeursinge, E., & Corboz-Warnery, A., (1999). *The primary triangle: A developmental systems view of mothers, fathers, and infants*. New York: Basic Books.

Flavell, J. H. (1985). *Cognitive development*. Englewood Cliffs, NJ: Prentice Hall.

Flavell, J. H., Flavell, E. R., & Green, F. L. (1987). Young children's knowledge about the apparent-real and the pretend-real distinctions. *Developmental Psychology*, *23*, 816–822.

Flavell, J. H., Flavell, E. R., Green, F. L., & Wilcox, S. A. (1981). The development of three spatial perspective-taking rules. *Child Development*, *52*, 356–358.

Fletcher, A. W. (2006). Clapping in chimpanzees: Evidence of exclusive hand preference in a spontaneous, bimanual gesture. *American Journal of Primatology*, *68*, 1081–1088.

Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, *15*, 447–452.

Fodor, J. (2000). *The mind doesn't work that way*. Cambridge, MA: MIT Press.

Fodor, J. A., & Pylyshyn, Z. W. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition*, *28*, 3–71.

Foley, R. A. (1987). *Another unique species*. Harlow, UK: Longman.

Foley, W. (1997). *Anthropological linguistics: An introduction*. London: Blackwell.

Ford, K. M., & Pylyshyn, Z. W. (Eds). (1996). *The robot's dilemma revisited: The frame problem in artificial intelligence*. Norwood, NJ: Ablex.

Foster, K. R., & Ratnieks, L. W. (2005). A new eusocial vertebrate? *Trends in Ecology and Evolution*, *20*, 363–364.

Frey, R., & Riede, T. (2003). Sexual dimorphism of the larynx of the Mongolian gazelle (*Procapra gutturosa* Pallas, 1777) (Mammalia, Artiodactyla, Bovidae). *Zoologischer Anzeiger*, *242*, 33–62.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences USA*, *103*, 2458–2463.

Friederici, A. D., Steinhauer, K., & Pfeifer, E. (2002). Brain signatures of artificial language processing: Evidence challenging the critical period hypothesis. *Proceedings of the National Academy of Sciences USA*, *99*, 529–534.

Fu, G., & Lee, K. (2007). Social grooming in the kindergarten: The emergence of flattery behavior. *Developmental Science*, *10*, 255–265.

Gácsi, M., Györi, B., Miklósi Á., Virányi, Z., Kubinyi, E., Topál, J., & Csányi, V. (2005). Species-specific differences and similarities in the behaviour of hand

raised dog and wolf puppies in social situations with humans. *Developmental Psychobiology*, *47*, 111–122.

Gaffan, D., & Harrison, S. (1991). Auditory-visual associations, hemispheric specialization and temporal frontal interaction in the rhesus monkey. *Brain*, *114*, 2133–2144.

Galef, B. G. (1992). The question of animal culture. *Human Nature*, *3*, 157–178.

Galef, B. G. (1995). Why behaviour patterns that animals learn socially are locally adaptive. *Animal Behaviour*, *49*, 1325–1334.

Galef, B. G. (2003). "Traditional" foraging behaviours of brown and black rats (*Rattus norvegicus* and *Rattus rattus*). In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 159–186). Cambridge, UK: Cambridge University Press.

Galef, B. G. (2004). Approaches to the study of traditional behaviors of free-living animals. *Learning and Behavior*, *32*, 53–61.

Galef, B. G., & Allen, C. (1995). A new model system for studying behavioural traditions in animals. *Animal Behaviour*, *50*, 705–717.

Galef, B. G., Manzig, L. A., & Field, R. M. (1986). Imitation learning in budgerigars: Dawson & Foss 1965 revisited. *Behavioural Processes*, *13*, 191–202.

Gallagher, S., & Marcel, A. J. (1999). The self in contextualized action. *Journal of Consciousness Studies*, *6*, 4–30.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallup, G. G., Anderson, J. R., & Shillito, D. J. (2002). The mirror test. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 325–333). Cambridge, MA: MIT Press.

Garcia Coll, C., Bearer, E. L., & Lerner, R. M. (Eds.). (2004). *Nature and nurture: The complex interplay of genetic and environmental influences on human behavior and development*. Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Gardner, B. T., & Gardner, R. A. (1971). Two-way communication with an infant chimpanzee. In A. M. Schrier & F. Stollnitz (Eds.), *Behavior of nonhuman primates: Modern research trends* (Vol. 4, pp. 117–184). New York: Academic Press.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science*, *165*, 664–672.

Gardner, R. A., & Gardner, B. T. (1989). A cross-fostering laboratory. In R. A. Gardner, B. T. Gardner, & T. E. van Cantfort (Eds.), *Teaching sign language to chimpanzees* (pp. 1–28). Albany, NY: State University of New York Press.

Garrod, S., & Doherty, G. (1994). Conversation, co-ordination and convention: An empirical investigation of how groups establish linguistic conventions. *Cognition*, *53*, 181–215.

Gaskins, S. (2006). Cultural perspectives on infant–caregiver interaction. In N. J. Enfield & S. C. Levinson (Eds.), *Roots of human sociality: Culture, cognition and interaction* (pp. 279–298). Oxford, UK: Berg.

Geissmann, T. (1984). Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pileatus x H. lar*). *Folia primatologica*, *24*, 216–235.

Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews*, *30*, 949–960.

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*, 755.

Gergely, G., & Csibra, G. (2005). The social construction of the cultural mind.

Imitative learning as a mechanism of human pedagogy. *Interaction Studies*, *6*, 463–481.

German, T. P., & Johnson, S. C. (2002). Function and the origins of the design stance. *Journal of Cognition and Development*, *3*, 279–300.

Ghazanfar, A. A., & Hauser, M. D. (1999). The neuroethology of primate vocal communication: Substrates for the evolution of speech. *Trends in Cognitive Sciences*, *3*, 377–384.

Ghazanfar, A. A., & Miller, C. T. (2006). Language evolution: Loquacious monkey brains? *Current Biology*, *16*, 879–881.

Ghazanfar, A. A., Smith-Rohrberg, D., & Hauser, M. D. (2001). The role of temporal cues in conspecific vocal recognition: Rhesus monkey orienting asymmetries to reversed calls. *Brain, Behavior and Evolution*, *58*, 163–172.

Ghazanfar, A. A., Turesson, H. K., Maier, J. X., van Dinther, R., Patterson, R. D., & Logothetis, N. K. (2007). Vocal-tract resonances as indexical cues in rhesus monkeys. *Current Biology*, *17*, 425–430.

Gifford, G. W., III, Hauser, M. D., & Cohen, Y. E. (2003). Discrimination of functionally referential calls by laboratory-housed rhesus macaques: Implications for neuroethological studies. *Brain, Behavior and Evolution*, *61*, 213–224.

Gilbert, M. (1990). Walking together: A paradigmatic social phenomenon. *Midwest Studies in Philosophy*, *15*, 1–14.

Gilbert, S. F. (2003). *Developmental biology*. Sunderland, MA: Sinauer Associates.

Gil-da-Costa, R., Braun, A., Lopes, M., Hauser, M. D., Carson, R. E., Herscovitch, P., & Martin, A. (2004). Toward an evolutionary perspective on conceptual representation: Species-specific calls activate visual and affective processing systems in the macaque. *Proceedings of the National Academy of Sciences USA*, *101*, 17516–17521.

Gil-da-Costa, R., & Hauser, M. D. (2006). Vervet monkeys and humans show brain asymmetries for processing conspecific vocalizations, but with opposite patterns of laterality. *Proceedings of the Royal Society of London, Series B*, *273*, 2313–2318.

Gil-Da-Costa, R., Martin, A., Lopes, M. A., Munoz, M., Fritz, J. B., & Braun, A. R. (2006). Species-specific calls activate homologs of Broca's and Wernicke's areas in the macaque. *Nature Neuroscience*, *9*, 1064–1070.

Gittelman, R., Mannuzza, S., Shenker, R., & Bonagura, N. (1985). Hyperactive boys almost grown up: I. Psychiatric status. *Archives of General Psychiatry*, *42*, 937–947.

Givón, T. (2002). *Bio-linguistics: The Santa Barbara lectures*. Amsterdam: John Benjamins.

Goldin-Meadow, S., & McNeill, D. (1999). The role of gesture and mimetic representation in making language the province of speech. In M. C. Corballis & S. E. G. Lea (Eds.), *The descent of mind* (pp. 155–172). Oxford, UK: Oxford University Press.

Gómez, J. C. (1996). Nonhuman primates' theories of (nonhuman primate) minds: Some issues concerning the origin of mindreading. In P. Carruthers & P. Smith (Eds.), *Theories of theories of mind* (pp. 330–343). Cambridge, UK: Cambridge University Press.

Gómez, J. C. (2005). Requesting gestures in captive monkeys and apes: Conditioned responses or referential behaviours? *Gesture*, *5*, 89–103.

Gómez, J. C., & Martín-Andrade, B. (2002). Possible precursors of pretend play in non-pretend actions of captive gorillas. In R. Mitchell (Ed.), *Pretending in animals and humans* (pp. 255–268). Cambridge, UK: Cambridge University Press.

Gómez, J. C., & Martín-Andrade, B. (2005). Fantasy play in animals. In A. Pellegrini

& P. K. Smith (Eds.), *The nature of play: Great apes and humans* (pp. 139–171). New York: Guilford Press.

Goodall, J. (1986). *The chimpanzees of gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University.

Goodall, J. V. L. (1973). Cultural elements in a chimpanzee community. In E. W. Menzel (Ed.), *Precultural primate behavior* (pp. 144–184). Basel, Switzerland: S. Karger.

Goodwin, B. C., & Trainor, L. E. H. (1983). The ontogeny and phylogeny of the pendactyl limb. In B. C. Goodwin, N. Holder, & C. C. Wylie (Eds.), *Development and evolution: The sixth symposium of the British Society for Developmental Biology* (pp. 75–98). Cambridge, UK: Cambridge University Press.

Goodwin, D., Bradshaw, J. W. S., & Wickens, S. M. (1997). Paedomorphosis affects visual signals of domestic dogs. *Animal Behaviour*, *53*, 297–304.

Gould, S. J. (1976). In defense of the analog: A commentary to N. Hotton. In R. B. Masterton, W. Hodos, & H. Jerison (Eds.), *Evolution, brain and behavior: Persistent problems* (pp. 175–179). New York: Wiley.

Gould, S. J. (1993). *Eight little piggies: Reflections in natural history*. New York: Norton.

Gouzoules, H., & Gouzoules, S. (1989). Design features and developmental modifications of pigtail macaque (*Macaca nemestrina*) agonistic screams. *Animal Behaviour*, *37*, 383–401.

Gouzoules, H., & Gouzoules, S. (1990). Matrilineal signatures in the recruitment screams of pigtail macaques, *Macaca nemestrina. Behaviour*, *115*, 327–347.

Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representation signalling in the recruitment of agonistic aid. *Animal Behaviour*, *32*, 182–193.

Graves, R., Goodglass, H., & Landis, T. (1982). Mouth asymmetry during spontaneous speech. *Neuropsychologia*, *20*, 371–381.

Gray, J. R., & Thompson, P. M. (2004). Neurobiology of intelligence: Science and ethics. *Nature Reviews Neuroscience*, *5*, 471–482.

Green, S. (1975). Dialects in Japanese monkeys: Vocal learning and cultural transmission of locale-specific behavior? *Zeitschrift für Tierpsychologie*, *38*, 304–314.

Greenberg, G., Partridge, T., Weiss, E., & Pisula, W. (2004). Comparative psychology, a new perspective for the 21st century: Up the spiral staircase. *Developmental Psychobiology*, *44*, 1–15.

Greenfield, P. M. (1991). Language, tools, and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, *14*, 531–550.

Greenfield, P. M., Keller, H., Fuligni, A., & Maynard, A. (2003). Cultural pathways through universal development. *Annual Review of Psychology*, *54*, 461–490.

Griffin, D. R. (2001). *Animal minds: Beyond cognition to consciousness*. Chicago: Chicago University Press.

Grossi, G., Semenza, C., Corazza, S., & Volterra, V. (1996). Hemispheric specialization for sign language. *Neuropsychologia*, *34*, 737–740.

Hacia, J. G. (2001). Genome of the apes. *Trends in Genetics*, *17*, 637–645.

Hagoort, P. (2005a). Broca's complex as the unification space for language. In A. Cutler (Ed.), *Twenty-first century psycholinguistics: Four cornerstones* (pp. 157–172). London: Lawrence Erlbaum Associates Ltd.

Hagoort, P. (2005b). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, *9*, 416–423.

Haight, W., & Miller, P. J. (1992). The development of everyday pretend play: A longitudinal study of mothers' participation. *Merrill Palmer Quarterly*, *38*, 331–349.

Hammerschmidt, K., Freudenstein, T., & Jürgens, U. (2001). Vocal development in squirrel monkeys. *Behaviour*, *138*, 1179–1204.

Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes in rhesus macaque "coo" vocalizations during early development. *Ethology*, *106*, 873–886.

Hare, B. (2007). From nonhuman to human mind: What changed and why? *Current Directions in Psychological Science*, *16*, 60–64.

Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour*, *65*, 131–142.

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*, 771–785.

Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, *61*, 139–151.

Hare, B., Call, J., & Tomasello, M. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition*, *101*, 495–514.

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*, 439–444.

Harman, G. (1978). Studying the chimpanzee's theory of mind. *Behavioral and Brain Sciences*, *4*, 576–577.

Harris, M. (1979). *Cultural materialism*. New York: Vintage.

Harris, P. L., & Kavanaugh, R. D. (1993). Young children's understanding of pretense. *Monographs of the Society for Research in Child Development*, *58*(1, Serial No. 231, v-92).

Hashima, P. Y., & Amato, P. R. (1994). Poverty, social support, and parental behavior. *Child Development*, *65*, 394–403.

Hatano, G., & Takahashi, K. (2005). Is shared intentionality widespread among and unique to humans? *Behavioral and Brain Sciences*, *28*, 703.

Hauser, M. D. (1988). How infant vervet monkeys learn to recognize starling alarm calls: The role of experience. *Behaviour*, *105*, 187–201.

Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (*Cercopithecus aethiops*) vocalizations. *Journal of Comparative Psychology*, *103*, 149–158.

Hauser, M. D. (1991). Sources of acoustic variation in rhesus macaque (*Macaca mulatta*) vocalizations. *Ethology*, *89*, 29–46.

Hauser, M. D. (1992). Articulatory and social factors influence the acoustic structure of rhesus monkey vocalizations: A learned mode of production? *Journal of the Acoustical Society of America*, *91*, 2175–2179.

Hauser, M. D. (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

Hauser, M. D. (1998). Functional referents and acoustic similarity: Field playback experiments with rhesus monkeys. *Animal Behaviour*, *55*, 1647–1658.

Hauser, M. D. (2000). *Wild minds: What animals really think*. New York: Henry Holt.

Hauser, M. D., Agnetta, B., & Perez, C. (1998). Orienting asymmetries in rhesus monkeys: Effect of time-domain changes on acoustic perception. *Animal Behaviour*, *56*, 41–47.

Hauser, M. D., & Akre, K. (2001). Asymmetries in the timing of facial and vocal expressions in rhesus monkeys: Implications for hemispheric specialization. *Animal Behaviour*, *61*, 391–408.

Hauser, M. D., & Andersson, K. (1994). Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: Field experiments. *Proceedings of the National Academy of Sciences USA*, *91*, 3946–3948.

Hauser, M., Chomsky, N., & Fitch, W. T. (2002). The language faculty: What is it, who has it, and how did it evolve? *Science*, *298*, 1569–1579.

Hauser, M. D., & Marler, P. (1993). Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behavioural Ecology*, *4*, 194–205.

Hauser, M. D., Teixidor, P., Field, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: Effects of food quantity and divisibility? *Animal Behaviour*, *45*, 817–819.

Hauser, M. D., & Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees: A preliminary report. *Folia primatologica*, *48*, 24–35.

Hayes, B. (1995). *Metrical stress theory: Principles and case studies*. Chicago: University of Chicago Press.

Hayes, C. (1951). *The ape in our house*. New York: Harper.

Hayes, C. (1952). *The ape in our house*. London: Gollancz.

Hayes, K. J., & Hayes, C. (1954). The cultural capacity of chimpanzee. *Human Biology*, *26*, 288–303.

Hayes, K. J., & Nissen, C. H. (1971). Higher mental functions of a home-raised chimpanzee. In A. M. Schrier & F. Stollnitz (Eds.), *Behavior of nonhuman primates: Modern research trends* (Vol. 4, pp. 59–115). New York: Academic Press.

Heffner, H. E., & Heffner, R. S. (1984). Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science*, *226*, 75–76.

Heinrich, B., & Bugnyar, T. (2007). Just how smart are ravens? *Scientific American*, *296*, 64–71.

Helfman, G. S., & Schultz, E. T. (1984). Social transmission of behavioral traditions in a coral reef fish. *Animal Behaviour*, *32*, 379–384.

Hepper, P. G. (1991). An examination of fetal learning before and after birth. *Irish Journal of Psychology*, *12*, 95–107.

Hewes, G. W. (1973). Primate communication and the gestural origin of language. *Current Anthropology*, *14*, 5–24.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour*, *46*, 999–1010.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*, 101–184.

Hill, R. S., & Walsh, C. A. (2005). Molecular insights into human brain evolution. *Nature*, *437*, 64–67.

Hirata, S., Watanabe, K., & Kawai, M. (2001). "Sweet-potato washing" revisited. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 487–508). Berlin, Germany: Springer.

Hodun, A., Snowdon, C. T., & Soini, P. (1981). Subspecific variation in the long calls of the tamarin, *Saguinus fuscicollis*. *Zeitschrift für Tierpsychologie*, *57*, 97–110.

Hoffmeyer, J. (1996). *Signs of meaning in the universe*. Bloomington, IN: Indiana University Press.

Hook-Costigan, M. A., & Rogers, L. J. (1998). Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia*, *36*, 1265–1273.

Hopkins, W. D., & Savage-Rumbaugh, E. S. (1991). Vocal communication as a

function of differential rearing experiences in *Pan paniscus*: A preliminary report. *International Journal of Primatology*, *12*, 559–583.

Hopkins, W. D., & Cantalupo, C. (2003). Brodmann's area 44, gestural communication and the emergence of right handedness in chimpanzees. Commentary on M. Corballis "From mouth to hand: The evolution of right handedness". *Behavioral and Brain Sciences*, *26*, 224–225.

Hopkins, W. D., & Cantero, M. (2003). From hand to mouth in the evolution of language: The influence of vocal behaviour on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science*, *6*, 55–61.

Hopkins, W. D., & de Waal, F. B. M. (1995). Behavioral laterality in captive bonobos (*Pan paniscus*). *International Journal of Primatology*, *2*, 261–276.

Hopkins, W. D., & Fernandez-Carriba, S. (2002). Laterality of communicative behaviours in nonhuman primates: A critical analysis. In L. J. Rogers & R. J. Andrew (Eds.), *Cerebral vertebrate lateralization* (pp. 445–479). New York: Cambridge University Press.

Hopkins, W. D., & Leavens, D. A. (1998). Hand use and gestural communication in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *112*, 95–99.

Hopkins, W. D., Russell, J. L., & Cantalupo, C. (2007). Neuroanatomical correlates of handedness for tool use in chimpanzees (*Pan troglodytes*): Implication for the evolution of language. *Psychological Science*, *18*, 971–977.

Hopkins, W. D., Russell, J. L., Freeman, H., Buehler, N., Reynolds, E., & Schapiro, S. J. (2005). The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychological Science*, *6*, 487–493.

Hopkins, W. D., Taglialatela, J. P., & Leavens, D. A. (2007). Chimpanzees differentially produce novels vocalizations to capture the attention of a human. *Animal Behaviour*, *73*, 281–286.

Hopkins, W. D., & Wesley, M. J. (2002). Gestural communication in chimpanzees (*Pan troglodytes*): The effect of situational factors on gesture type and hand use. *Laterality*, *7*, 19–30.

Hopper, L., Spiteri, A., Lambeth, S. P., Schapiro, S., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, *73*, 1021–1032.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*, 164–181.

Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2007). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences USA*, *103*, 13878–13883.

Horowitz, A. C. (2003). Do humans ape? Or do apes human? Imitation and intention in humans (*Homo sapiens*) and other animals. *Journal of Comparative Psychology*, *117*, 325–336.

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication in response to the attentional status of a human. *Journal of Comparative Psychology*, *115*, 337–343.

Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: Evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*, *10*, 55–62.

Hrdy, S. (1999). *Mother Nature: A history of mothers, infants, and natural selection*. New York: Pantheon Books.

Hrdy, S. B. (2005a). Comes the child before the man: Cooperative breeding and the evolution of prolonged post-weaning dependence. In B. Hewlett & M. Lamb (Eds.), *Hunter-gatherer childhoods: Evolutionary, developmental, and cultural perspectives* (pp. 65–91). New Brunswick, NJ: Aldine/Transactions.

Hrdy, S. B. (2005b). Evolutionary context of human development: The cooperative breeding model. In C. S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S. W. Porges, & N. Sachser (Eds.), *Attachment and bonding: A new synthesis; From the 92nd Dahlem workshop report* (pp. 9–32). Cambridge, MA: MIT Press.

Huang-Pollock, C. L., & Nigg, J. T. (2003). Searching for the attention deficit in attention deficit hyperactivity disorder: The case of visuospatial orienting. *Clinical Psychology Review*, *23*, 801–830.

Huber, L. (1998). Movement imitation as faithful copying in the absence of insight. *Behavioral and Brain Sciences*, *21*, 694.

Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis. Animal Behaviour*, *62*, 945–954.

Huffman, M. A., & Hirata, S. (2004). An experimental study of leaf swallowing in captive chimpanzees: Insights into the origin of a self-medicative behaviour and the role of social learning. *Primates*, *45*, 113–118.

Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, *58*, 133–148.

Hunt, K. D., & McGrew, W. C. (2002). Chimpanzees in the dry habitats of Assirik, Senegal, and Semliki Wildlife Reserve, Uganda. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 35–51). Cambridge, UK: Cambridge University Press.

Hurford, J. R. (2007). *The origins of meaning*. Oxford, UK: Oxford University Press.

Hurley, S. (2003). Animal action in the space of reason. *Mind and Language*, *18*, 231–257.

Ingold, T. (2001). The uses and abuses of ethnography. *Behavioral and Brain Sciences*, *24*, 337.

Inoue-Nakamura, N. (2001). Mirror self-recognition in primates: An ontogenetic and a phylogenetic approach. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 297–312). Tokyo: Springer-Verlag.

Insko, C. A., Gilmore, R., Drenan, S., Lipsitz, A., Moehle, D., & Thibaut, J. (1983). Trade versus exploration in open groups: A comparison of two types of social power. *Journal of Personality and Social Psychology*, *44*, 977–999.

Insko, C. A., Thibaut, J. W., Moehle, D., Wilson, M., Diamond, W. D., Gilmore, R., et al. (1980). Social evolution and the emergence of leadership. *Journal of Personality and Social Psychology*, *39*, 431–448.

Iverson, J. M., & Thelen, E. (1999). Hand, mouth, and brain: The dynamic emergence of speech and gesture. *Journal of Consciousness Studies*, *6*, 19–40.

Jablonka, E., & Lamb, M. (2007). Bridging the gap: The developmental aspects of evolution. *Behavioral and Brain Sciences*, *30*, 353–365.

Jackendoff, R. (2002). *Foundations of language*. New York: Oxford University Press.

Jackendoff, R., & Pinker, S. (2005). The nature of the language faculty and its implications for the evolution of language (Reply to Fitch, Hauser, & Chomsky). *Cognition*, *97*, 211–225.

Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in Cognitive Sciences*, *9*, 21–25.

Jacobs, R. C., & Campbell, D. T. (1961). The perpetuation of an arbitrary tradition through several generations of laboratory microculture. *Journal of Abnormal and Social Psychology*, *62*, 649–658.

Jamieson, D. (2002). *Morality's progress: Essays on humans, other animals, and the rest of nature*. Oxford, UK: Oxford University Press.

Janik, V. M., & Slater, P. B. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, 59–99.

Jenkins, L. (2000). *Biolinguistics: Exploring the biology of language*. New York: Cambridge University Press.

Jenkins, L. (Ed.). (2004). *Variation and universals in biolinguistics*. Amsterdam: Elsevier.

Johansson, S. (2005). *Origins of language: Constraints on hypotheses*. Amsterdam: John Benjamins.

Joshi, A. K., Vijay-Shanker, K., & Weir, D. (1991). The convergence of mildly context-sensitive formalisms. In P. Sells, S. Shieber, & T. Wasow (Eds.), *Processing of linguistic structure* (pp. 31–81). Cambridge, MA: MIT Press.

Joyce, S. M., & Snowdon, C. T. (2007). Developmental changes in food transfers in cotton-cop tamarins (*Saguinus oedipus*). *American Journal of Primatology*, *69*, 1–11.

Jürgens, U. (2002). Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Review*, *26*, 235–258.

Jürgens, U., & Zwirner, P. (2000). Individual hemispheric asymmetry in vocal fold control of the squirrel monkey. *Behavioural Brain Research*, *109*, 213–217.

Kagan, J. (1981). *The second year: The emergence of self-awareness*. Cambridge, MA: Harvard University Press.

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: Evidence for fast mapping. *Science*, *304*, 1682–1683.

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition*, *7*, 216–223.

Karin D'Arcy, M. R. (2005). The modern role of Morgan's canon in comparative psychology. *International Journal of Comparative Psychology*, *18*, 179–201.

Kawai, M. (1965). Newly-acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, *6*, 1–30.

Kawai, M., Watanabe, K., & Mori, A. (1992). Precultural behaviors observed in free-ranging Japanese monkeys on Koshima Islet over the past 25 years. *Primate Report*, *32*, 143–153.

Kawamura, S. (1959). The process of subculture propagation among Japanese macaques. *Primates*, *2*, 43–60.

Kelemen, D. (1999). The scope of teleological thinking in preschool children. *Cognition*, *70*, 241–272.

Keller, H., Lohaus, A., Kuensemueller, P., Abels, M., Yovsi, R., Voelker, S., et al. (2004). The bio-culture of parenting: Evidence from five cultural communities. *Parenting: Science and Practice*, *4*, 25–50.

Kellogg, W. N., & Kellogg, L. A. (1933). *The ape and the child: A study of environmental influence upon early behavior*. New York: Whittlesey House.

Kendon, A. (1991). Some considerations for a theory of language origins. *Man*, *26*, 199–221.

Kenstowicz, M. J. (1994). *Phonology in generative grammar*. Oxford, UK: Blackwell.

Kimura, D. (1973). Manual activity during speaking: I. Right-handers. *Neuropsychologia*, *11*, 45–50.

Kimura, D. (1993). *Neuromotor mechanisms in human communication*. Oxford, UK: Oxford University Press.

King, B. J. (1994). Primate infants as skilled information gatherers. *Pre-Perinatal Psychology Journal*, *8*, 287–307.

King, B. J. (1999). New directions in the study of primate learning. In H. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 17–32). Cambridge, UK: Cambridge University Press.

King, B. J. (2004). *The dynamic dance: Nonvocal communication in African great apes*. Cambridge, MA: Harvard University Press.

Kirby, S. (2000). Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. In C. Knight, M. Studdert-Kennedy, & J. Hurford (Eds.), *The evolutionary emergence of language: Social functions and the origins of linguistic form* (pp. 303–323). Cambridge, UK: Cambridge University Press.

Kirby, S., Dowman, M., & Griffiths, T. L. (2007). Innateness and culture in the evolution of language. *Proceedings of the National Academy of Sciences USA*, *104*, 5241–5245.

Kirby, S., Smith, K., & Brighton, H. (2004). From UG to universals: Linguistic adaptation through iterated learning. *Studies in Language*, *2*, 587–607.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*)—Evidence from playback experiments. *Ethology*, *112*, 346–354.

Kirschner, M. W., & Gerhart, J. C. (2005). *The plausibility of life: Resolving Darwin's dilemma*. London: Yale University Press.

Kirsh, D. (1995). The intelligent use of space. *Artificial Intelligence*, *73*, 31–68.

Kirsh, D. (2005). Metacognition, distributed cognition and visual design. In P. Gärdenfors & P. Johansson (Eds.), *Cognition, education, and communication technology* (pp. 147–180). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Klein, W., & Dittmar, N. (1979). *Developing grammar: The acquisition of German syntax by foreign workers*. Berlin, Germany: Springer.

Knecht, S., Deppe, M., Draeger, B., Bobe, L., Lohman, H., Ringelstein, E. B., & Henningsen, H. (2000). Language lateralization in healthy right-handers. *Brain*, *123*, 74–81.

Knott, C. D. (2001). Female reproductive ecology in apes. In P. T. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 429–463). Hawthorne, NJ: Aldine de Gruyter.

Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron*, *50*, 963–974.

Koehler, W. (1927). *The mentality of apes* (2nd ed.). London: Kegan Paul, Trench, Trubner & Co.

Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846–848.

Köhler, W. (1926). *The mentality of apes*. London: Routledge & Kegan Paul.

Kojima, S. (2003). *A search for the origins of human speech: Auditory and vocal functions of the chimpanzee*. Kyoto, Japan: Kyoto University Press.

Kostan, K. M., & Snowdon, C. T. (2002). Attachment and social preferences in cooperatively-reared cotton-top tamarins. *American Journal of Primatology*, *57*, 131–139.

Kralik, J., Hauser, M. D., & Zimlicki, R. (2002). The relationship between problem solving and inhibitory control: Cotton-top tamarin (*Saguinus oedipus*) performance in a reversed contingency task. *Journal of Comparative Psychology*, *116*, 39–50.

Kramer, K. L. (2005). Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*, 224–237.

Krause, M. A., & Fouts, R. S. (1997). Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, *111*, 330–336.

Kroeber, A. L. (1928). Sub-human cultural beginnings. *Quarterly Review of Biology*, *3*, 325–342.

Kruetzen, M., van Schaik, C., & Whiten, A. (2007). The animal cultures debate: Response to Laland and Janik. *Trends in Ecology and Evolution*, *22*, 6.

Kummer, H. (1968). *Social organization of Hamadryas baboons*. Chicago: University of Chicago Press.

Kummer, H. (1971). *Primate societies*. Chicago: Aldine.

Kummer, H. (1978) On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information*, *17*, 687–705.

Kuper, A. (1999). *Culture: The anthropologist's account*. Cambridge, MA: Harvard University Press.

Labov, W. (1972). *Language in the inner city: Studies in the black English vernacular*. Philadelphia: University of Pennsylvania Press.

Laiolo, P., & Jovani, R. (2007). The emergence of animal culture conservation. *Trends in Ecology and Evolution*, *22*, 5.

Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology*, *12*, 150–159.

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology and Evolution*, *21*, 542–547.

Laland, K. N., & Janik, V. (2007). Response to Kruetzen et al.: Further problems with the "method of exclusion". *Trends in Ecology and Evolution*, *22*, 7.

Laland, K. N., & Plotkin, H. C. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning and Behavior*, *18*, 246–251.

Laland, K. N., & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, *53*, 1161–1169.

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioural Ecology*, *9*, 493–499.

Landau, B., & Gleitman, L. (1985). *Language and experience: Evidence from the blind child*. Cambridge, MA: Harvard University Press.

Landau, B., & Jackendoff, R. (1993). What and where in spatial language and spatial cognition. *Behavioral and Brain Sciences*, *16*, 217–265.

Langen, T. A. (2000). Prolonged offspring dependence and cooperative breeding in birds. *Behavioural Ecology*, *11*, 367–377.

Langer, J. (1998). Uniquely to what ends? Comments on Michael Tomasello's "Uniquely primate, uniquely human". *Developmental Science*, *1*, 22–24.

Langer, S. K. (1942). *Philosophy in a new key: A study in the symbolism of reason, rite and art*. Cambridge, MA: Harvard University Press.

Langer, S. K. (1962). *Philosophical sketches*. Baltimore: Johns Hopkins Press.

Leadbeater, E., Raine, N. E., & Chittka, L. (2006). Social learning: Ants and the meaning of teaching. *Current Biology*, *16*, R323–R325.

Leahy Warren, P. (2005). First-time mothers: Social support and confidence in infant care. *Journal of Advanced Nursing*, *50*, 479–488.

Learmonth, A. E., Lamberth, R., & Rovee-Collier, C. (2005). The social context of imitation in infancy. *Journal of Experimental Child Psychology*, *91*, 297–314.

Leavens, D. A. (2003). Integration of visual and vocal communication: Evidence for Miocene origins. Commentary on M. Corballis "From mouth to hand: The evolution of right handedness". *Behavioral and Brain Sciences*, *26*, 232–233.

Leavens, D. A. (2004). Manual deixis in apes and humans. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*, *5*, 387–408.

Leavens, D. A. (2006). It takes time and experience to learn how to interpret gaze in mentalistic terms. *Infant and Child Development*, *15*, 187–190.

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*, 813–822.

Leavens, D. A., & Hopkins, W. D. (1999). The whole hand point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology*, *113*, 417–425.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *110*, 346–353.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science*, *14*, 185–189.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2007, March). *Pointing in chimpanzees: Exploring issues of epigenesis and evolutionary origins*. Abstracts from The Mind of the Chimpanzee meeting, Lincoln Park Zoo, Chicago.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2008). The heterochronic origins of explicit reference. In J. Zlatev, T. P. Racine, C. Sinha, & E. Itkonen (Eds.), *The shared mind: Perspectives on intersubjectivity* (pp. 187–214). Amsterdam: John Benjamins.

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *118*, 48–57.

Leavens, D. A., Hostetter, A. B., Wesley, M. J., & Hopkins, W. D. (2004). Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *67*, 467–476.

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development*, *76*, 291–306.

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behaviour and Evolution*, *63*, 233–246.

Lemasson, A., Gautier, J. P., & Hausberger, M. (2003). Vocal similarities and social bonds in Campbell's monkey (*Cercopithecus campbelli*). *Comptes Rendus Biologies*, *326*, 1185–1193.

Lemasson, A., Hausberger, M., & Zuberbühler, K. (2005). Socially meaningful vocal plasticity in adult Campbell's monkeys (*Cercopithecus campbelli*). *Journal of Comparative Psychology*, *119*, 220–229.

Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.

Levinson, St. C. (2001). *Space, language and cognition: Explorations in cognitive diversity*. Cambridge, MA: Cambridge University Press.

Lewis, D. K. (1969). *Convention: A philosophical study*. Cambridge, MA: Harvard University Press.

Liebal, K., Call, J., & Tomasello, M. (2004). Chimpanzee gesture sequences. *Primates*, *64*, 377–396.

Liebal, K., Pika, S., Call., J., & Tomasello, M. (2004). To move or not to move: How apes alter the attentional state of others. *Interaction Studies*, *5*, 199–219.

Liebal, K., Pika, S., & Tomasello, M. (2004). Social communication in siamangs (*Symphalangus Syndactulus*): Use of gestures and facial expressions. *Primates*, *45*, 41–57.

Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture*, *6*, 1–38.

Lieberman, D. E., & McCarthy, R. C. (1999). The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions. *Journal of Human Evolution*, *36*, 487–517.

Lieberman, D. E., McCarthy, R. C., Hiiemae, K. M., & Palmer, J. B. (2001). Ontogeny of postnatal hyoid and larynx descent in humans. *Archives of Oral Biology*, *46*, 117–128.

Lieberman, P. (1975). *On the origins of language*. New York: Macmillan.

Lieberman, P. (1984). *The biology and evolution of language*. Cambridge, MA: Harvard University Press.

Lieberman, P. (1998a). *Eve spoke: Human language and human evolution*. New York: W. W. Norton & Company.

Lieberman, P. (1998b). On the evolution of human syntactic ability: Its pre-adaptive bases, motor control and speech. *Journal of Human Evolution*, *14*, 657–668.

Lieberman, P. (2000). *Human language and our reptilian brain: The subcortical bases of speech, syntax and thought*. Cambridge, MA: Harvard University Press.

Lieberman, P. (2006). *Toward an evolutionary biology of language*. Cambridge, MA: Harvard University Press.

Lieberman, P., Klatt, D. H., & Wilson, W. H. (1969). Vocal tract limitations on the vowel repertoires of rhesus monkeys and other nonhuman primates. *Science*, *164*, 1185–1187.

Liszkowski, U. (2005). Human twelve-month-olds point cooperatively to share interest with and provide information for a communicative partner. *Gesture*, *5*, 135–154.

Liszkowski, U., Carpenter, M., Henning, A., Striano, T., & Tomasello, M. (2004). Twelve-month-olds point to share attention and interest. *Developmental Science*, *7*, 297–307.

Locke, J. L., Bekken, K. E., McMinn-Larson, L., & Wein, D. (1995). Emergent control of manual and vocal-motor activity in relation to the development of speech. *Brain and Language*, *51*, 498–508.

Loevenbruck, H., Baciu, M., Segebarth, C., & Abry, C. (2005). The left inferior frontal gyrus under focus: An fMRI study of the production of deixis via syntactic extraction and prosodic focus. *Journal of Neurolinguistics*, *18*, 237–258.

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*, 673–683.

Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. *Symposia of the Society for Experimental Biology*, *4*, 221–268.

Mace, R., & Sear, R. (2005). Are humans cooperative breeders? In E. Voland, A. Chasiotis, & W. Schiefenhövel (Eds.), *Grandmotherhood: The evolutionary significance of the second half of female life* (pp. 143–159). Piscataway, NJ: Rutgers University Press.

Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology*, *86*, 177–190.

Machado, A., Lourenço, O., & Silva, F. J. (2000). Facts, concepts and theories: The shape of psychology's epistemic triangle. *Behavior and Philosophy*, *28*, 1–40.

MacKay, D. (2003). *Information theory, inference, and learning algorithms*. Cambridge, UK: Cambridge University Press.

MacNeilage, P. F. (1998). The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences*, *21*, 499–546.

Maestripieri, D. (2005). Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*): Use of signals in relation to dominance and social context. *Gesture*, *5*, 55–71.

Maestripieri, D., Megna, N. L., & Ross, S. K. (2002). Mother–infant interactions in Western Lowland gorillas (*Gorilla gorilla gorilla*): Spatial relationships, communication, and opportunities for social learning. *Journal of Comparative Psychology*, *116*, 219–277.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, S. P., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*, 227–233.

Malle, F. B., Moses, J. L., & Baldwin, D. A. (2002). *Intentions and intentionality: Foundations of social cognition*. Cambridge, MA: MIT Press.

Marler, P. (1991). The instinct to learn. In S. Carey & R. Gelman (Eds.), *The epigenesis of mind: Essays on biology and cognition* (pp. 37–66). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Marler, P. (2000). Origins of music and speech: Insights from animals. In N. L. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 31–48). Cambridge, MA: MIT Press.

Marler, P., & Slabbekoorn, H. (2004). *Nature's music: The science of birdsong*. New York: Academic Press.

Maros, K., Dóka, A., & Miklósi, Á. (2008). Behavioural correlation of heart rate changes in family dogs. *Applied Animal Behaviour*, *109*, 329–341.

Marr, D. (1982). *Vision*. New York: W. H. Freeman & Co.

Marshall, A., Wrangham, R., & Arcadi, A. C. (1999). Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour*, *58*, 825–830.

Matsuzawa, T. (2007). Comparative cognitive development. *Developmental Science*, 10, 97–103.

Matsuzawa, T. (2006). Evolutionary origins of the human mother-infant relationship. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 127–141). Tokyo: Springer.

Mayr, E. (1974). Teleological and teleonomic: A new analysis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Boston studies in the philosophy of science: Methodological and historical essays in the natural and social sciences* (Vol. XIV, pp. 91–117). Dordrecht, The Netherlands: Kluwer.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge, UK: Cambridge University Press.

McGrew, W. C. (1998). Culture in nonhuman primates? *Annual Review of Anthropology*, *27*, 301–328.

McGrew, W. C. (2003). Ten dispatches from the chimpanzee culture wars. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture and individualized societies* (pp. 419–439). Cambridge, MA: Harvard University Press.

McGrew, W. C. (2004). *The cultured chimpanzee: Reflections on cultural primatology*. Cambridge, UK: Cambridge University Press.

McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., & Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology*, *18*, 353–374.

McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. G. (2001). Intergroup differences in a social custom of wild chimpanzees: The grooming-hand-clasp. *Current Anthropology*, *42*, 148–153.

McGrew, W. C., & Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man*, *13*, 234–251.

McNeill, D. (1992). *Hand and mind*. Chicago: University of Chicago Press.

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate social group: The relation between visual attention and hierarchical ranks. *Animal Cognition*, *1*, 65–70.

Meguerditchian, A., & Vauclair, J. (2006). Baboons communicate with their right hand. *Behavioural Brain Research*, *171*, 170–174.

Mehler, J., Jusczyk, P., Lambertz, G., Halsted, N., Bertoncini, J., & Amiel-Tison, C. (1988). A precursor of language acquisition in young infants. *Cognition*, *29*, 143–178.

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, *30*, 331–351.

Meltzoff, A. N. (1995). What infant memory tells us about infantile amnesia: Long-term recall and deferred imitation. *Journal of Experimental Child Psychology*, *59*, 497–515.

Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, *198*, 75–78.

Mendes, N., Rakoczy, H., & Call, J. (2008). Ape metaphysics: Object individuation without language. *Cognition*, *106*, 730–749.

Menzel, E. W. (Ed.). (1973). *Precultural primate behavior*. Basel, Switzerland: S. Karger.

Menzel, E. W., Davenport, R. K., & Rogers, C. M. (1972). Protocultural aspects of chimpanzees' responsiveness to novel objects. *Folia Primatologica*, *17*, 161–170.

Mesoudi, A., & Whiten, A. (2004). The hierarchical transformation of event knowledge in human cultural transmission. *Journal of Cognition and Culture*, *4*, 1–24.

Mesoudi, A., Whiten, A., & Dunbar, R. (2006). A bias for social information in human cultural transmission. *British Journal of Psychology*, *97*, 405–423.

Michel, G. (2007, March–April). *Molecular biology, statistical packages, computer software, and a conceptual framework provide the means for doing "real"*

developmental research. Paper presented at the meeting of the Society for Research in Child Development, Boston.

Miklósi, Á. (1999). The ethological analysis of imitation. *Biological Reviews*, *74*, 347–374.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans but dogs do. *Current Biology*, *13*, 763–766.

Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, *9*, 81–93.

Miklósi, Á., Topál, J., & Csányi, V. (2004). Comparative social cognition: What can dogs teach us? *Animal Behaviour*, *67*, 995–1004.

Miles, H. L. (1990). The cognitive foundations for reference in a signing orangutan. In S. T. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 511–539). Cambridge, UK: Cambridge University Press.

Miller, G. A., & Chomsky, N. (1963). Finitary models of language users. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology* (pp. 419–492). New York: Wiley.

Mills, M., & Melhuish, E. (1974). Recognition of mother's voice in early infancy. *Nature*, *252*, 123–124.

Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: Tests of three hypotheses. *Behaviour*, *135*, 1041–1064.

Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., & Byrne, R. (1992). Dialects in wild chimpanzees? *American Journal of Primatology*, *27*, 233–243.

Mitani, J. C., Hunley, K. L., & Murdoch, M. E. (1999). Geographic variation in the calls of wild chimpanzees: A reassessment. *American Journal of Primatology*, *47*, 133–151.

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, *45*, 735–746.

Mitchell, R. W. (Ed.). (2002). *Pretending and imagination in animals and children*. Cambridge, UK: Cambridge University Press.

Mitchell, R. W. (2004). Controlling the dog, pretending to have a conversation, or just being friendly? Influences of sex and familiarity on Americans' talk to dogs during play. *Interaction Studies*, *5*, 99–129.

Mithen, S. (2001). The evolution of imagination: An archaeological perspective. *Substance*, *30*, 28–54.

Montminy, M. (2005). What use is Morgan's canon? *Philosophical Psychology*, *18*, 399–414.

Moore, C., & Corkum, V. (1994). Social understanding at the end of the first year of life. *Developmental Review*, *14*, 349–372.

Moore, K., Cleland, J., & McGrew, W. C. (1991). Visual encounters between families of cotton-top tamarins (*Saguinus oedipus*). *Primates*, *32*, 23–33.

Morgan, C. L. (1903). *An introduction to comparative psychology*. London: Walter Scott Publishing.

Morgan, E. (1997). *The aquatic ape hypothesis*. London: Souvenir Press.

Morgan, L. H. (1868). *The American beaver and his works*. Philadelphia: Lippincott.

Morris, R. D., Hopkins, W. D., & Bolser-Gilmore, L. (1993). Assessment of hand preference in two language-trained chimpanzees (*Pan troglodytes*): A multimethod analysis. *Journal of Clinical and Experimental Neuropsychology*, *15*, 487–502.

Moura, A. C. A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*, 1909.

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science*, *312*, 1038–1040.

Mundy, P., Delgado, C., Block, J., Venezia, M., Hogan, A., & Seibert, J. (2003). *A manual for the abridged Early Social Communication Scales (ESCS)*. Coral Gables, FL: University of Miami, Department of Psychology.

Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation in a neonatal chimpanzee (*Pan troglodytes*). *Developmental Science*, *7*, 437–442.

Nakamura, M. (2002). Grooming-hand-clasp in Mahale M Group chimpanzees: Implications for culture in social behaviours. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 71–83). Cambridge, UK: Cambridge University Press.

Neilson, J. C., Hart, B. L., Cliff, K. D., & Ruehl, W. W. (2001). Prevalence of behavioral changes associated with age-related cognitive impairment in dogs. *Journal of the American Veterinary Medical Association*, *218*, 1787–1791.

Neiworth, J. J., Burman, M. A., Basile, B. M., & Lickteig, M. T. (2002). Use of experimenter-given cues in visual co-orienting and in an object-choice task by a New World Monkey species, Cotton Top Tamarins (*Saguinus Oedipus*). *Journal of Comparative Psychology*, *116*, 3–11.

Newmeyer, F. J. (1991). Functional explanation in linguistics and the origin of language. *Language and Communication*, *11*, 1–28.

Nicol, C. J., & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal Behaviour*, *47*, 1289–1296.

Nishida, T. (1987). Local traditions and cultural transmission. In B. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, & T. Struhsaker (Eds.), *Primate societies* (pp. 462–474). Chicago: University of Chicago Press.

Nishida, T., & Turner, L. A. (1996). Food transfer between mother and infant chimpanzees of the Mahale Mountains National Park, Tanzania. *International Journal of Primatology*, *17*, 947–968.

Okanoya, K. (2002). Sexual display as a syntactic vehicle: The evolution of syntax in birdsong and human language through sexual selection. In A. Wray (Ed.), *The transition to language* (pp. 46–63). Oxford, UK: Oxford University Press.

Opie, I., & Opie, P. (1987). *The language and lore of school children*. Oxford, UK: Oxford University Press.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). Evidence of limited modification in the vocalizations of cross-fostered rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology: Human origins* (pp. 257–270). Tokyo: University of Tokyo Press.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus and Japanese macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*, 389–406.

Panger, M. A., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., MacKinnon, K. C., & Baker, M. (2002). Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, *119*, 52–66.

Parker, S. T., & McKinney, M. L. (1999). *Origins of intelligence: The evolution of*

cognitive development in monkeys, apes, and humans. Baltimore and London: Johns Hopkins University Press.

Patterson, F. (1978). Linguistic capabilities of a lowland gorilla. In F. C. C. Peng (Ed.), *Sign language and language acquisition in man and ape* (pp. 161–201). Boulder, CO: Westview Press.

Pepperberg, I. M., & Wilcox, S. E. (2000). Evidence for a form of mutual exclusivity during label acquisition by grey parrots (*Psittacus erithacus*)? *Journal of Comparative Psychology*, *114*, 219–231.

Perner, J. (1991). *Understanding the representational mind*. Cambridge, MA: MIT Press.

Perner, J., Sprung, M., Zauner, P., & Haider, H. (2003). Want that is understood well before say that, think that, and false belief: A test of de Villiers's linguistic determinism on German-speaking children. *Child Development*, *74*, 179–188.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., et al. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, *44*, 241–268.

Petersen, M. R., Beecher, M. D., Zoloth, S. R., Moody, D. B., & Stebbins, W. C. (1978). Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). *Science*, *202*, 324–327.

Petrides, M., Cadoret G., & Mackey S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, *435*, 1235–1238.

Phillips, W., & Santos, L. (2007). Evidence of kind representations in the absence of language: Experiments with rhesus monkeys (*Macaca mulatta*). *Cognition*, *102*, 455–463.

Piaget, J. (1952). *The origins of intelligence in children*. New York: Basic Books.

Pika, S., Liebal, K., Call, J., & Tomasello, M. (2005). The gestural communication of apes. *Gesture*, *5*, 41–56.

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): Gestural repertoire, learning and use. *American Journal of Primatology*, *60*, 95–111.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): Gestural repertoire and use. *American Journal of Primatology*, *65*, 39–51.

Pika, S., & Mitani, J. C. (2006). Referential gesturing in wild chimpanzees (*Pan troglodytes*). *Current Biology*, *16*, 191–192.

Pinker, S. (1994). *The language instinct*. New York: William Morrow & Company, Inc.

Pinker, S. (2003). Language as an adaptation to the cognitive niche. In M. H. Christiansen & S. Kirby (Eds.), *Language evolution: The states of the art* (pp. 16–37). Oxford, UK: Oxford University Press.

Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences*, *13*, 507–508.

Pinker, S., & Jackendoff, R. (2005). The faculty of language: What's special about it? *Cognition*, *95*, 201–236.

Piveteau, J. (1991). *La main et l'hominisation*. Paris: Masson.

Ploog, D. (1981). Neurobiology of primate audio-vocal behaviour. *Brain Research Reviews*, *3*, 35–61.

Pollick, A. S., & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences USA*, *104*, 8184–9189.

Pongrácz, P., Miklósi, Á., Kubinyi, E., Gurobi, K., Topál, J., & Csányi, V. (2001). Social learning in dogs: I. The effect of a human demonstrator on the

performance of dogs (*Canis familiaris*) in a detour task. *Animal Behaviour*, *62*, 1109–1117.

Pongrácz, P., Miklósi, Á., Tímár-Geng, K., & Csányi, V. (2004). Verbal attention getting as a key factor in social learning between dog (*Canis familiaris*) and human. *Journal of Comparative Psychology*, *118*, 375–383.

Pongrácz, P. Miklósi, Á., Vida, V., & Csányi, V. (2005). The pet dog's ability for learning from a human demonstrator in a detour task is independent from the breed and age. *Applied Animal Behaviour Science*, *90*, 309–323.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*, 455–456.

Pöppel, E. (1994). Temporal mechanisms in perception. *International Review of Neurobiology*, *37*, 185–202.

Pöppel, E. (1997). A hierarchical model of temporal perception. *Trends in Cognitive Science*, *1*, 56–61.

Poremba, A., Malloy, M., Saunders, R. C., Carson, R. E., Herscovitch, P., & Mishkin, M. (2004). Species-specific calls evoke asymmetric activity in the monkey's temporal poles. *Nature*, *427*, 448–451.

Portner, P. H. (2005). *What is meaning: Fundamentals of formal semantics*. Oxford, UK: Blackwell.

Povinelli, D., Bering, J. M., & Giambrone, S. (2003). Chimpanzee "pointing": Another error of the argument by analogy? In S. Kita (Ed.), *Pointing: Where language, culture, and cognition meet* (pp. 35–68). Hillsdale, NJ: Erlbaum.

Povinelli, D. J., & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, *61*, 1–152.

Povinelli, D. J., & O'Neill, D. K. (2000). Do chimpanzees use their gestures to instruct each other? In S. Baron-Cohen, H. Tager, & D. J. Cohen (Eds.), *Understanding other minds* (2nd ed), (pp. 459–487). Oxford, UK: Oxford University Press.

Povinelli, D. J., & Prince, C. G. (1998). When self met other. In M. D. Ferrari & R. J. Sternberg (Eds.), *Self-awareness: Its nature and development* (pp. 37–107). New York: Guilford Press.

Premack, D. (1971). Language in chimpanzee? *Science*, *172*, 808–822.

Premack, D. (1972). Concordant preferences as a precondition for affective but not for symbolic communication (or how to do experimental anthropology). *Cognition*, *1*, 251–264.

Premack, D. (1976). *Intelligence in ape and man*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Premack, D., & Hauser, M. C. (2005). Why animals do not have culture. In S. C. Levinson & P. Jaisson (Eds.), *The evolution of culture: A Fyssen Foundation symposium* (pp. 275–278). Cambridge, MA: MIT Press.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, *1*, 515–526.

Preuschoft, S., & van Schaik, C. P. (2000). Dominance, social relationships and conflict management. In F. Aureli & F. B. M. de Waal (Eds.), *Conflict management* (pp. 77–105). Berkeley, CA: California University Press.

Price, E., & Caldwell, C. A. (2007). Artificially generated cultural variation between two groups of captive monkeys, *Colobus guereza kikuyuensis*. *Behavioural Processes*, *74*, 13–20.

Quiatt, D., & Reynolds, V. (1993). *Primate behaviour: Information, social knowledge, and the evolution of culture*. Cambridge, UK: Cambridge University Press.

Rachels, J. (1990). *Created from animals: The moral implications of Darwinism*. Oxford, UK: Oxford University Press.

Rainey, H., Zuberbühler, K., & Slater, P. J. B. (2004a). Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society of London, Series B*, *271*, 755–759.

Rainey, H., Zuberbühler, K., & Slater, P. J. B. (2004b). The responses of black-casqued hornbills to predator vocalizations and primate alarm calls. *Behaviour*, *141*, 1263–1277.

Rakoczy, H. (2006). Pretend play and the development of collective intentionality. *Cognitive Systems Research*, *7*, 113–127.

Rakoczy, H. (2007). Play, games, and the development of collective intentionality. In C. Kalish & M. Sabbagh (Eds.), *Conventionality in cognitive development: How children acquire representations in language, thought and action* (New directions in child and adolescent development No. 115, pp. 53–67). San Francisco: Jossey-Bass.

Rakoczy, H. (in press). Taking fiction seriously: Young children understand the normative structure of joint pretend games. *Developmental Psychology*.

Rakoczy, H., & Tomasello, M. (2006). Two-year-olds grasp the intentional structure of pretense acts. *Developmental Science*, *9*, 558–565.

Rakoczy, H., & Tomasello, M. (2007). The ontogeny of social ontology: Steps to shared intentionality and status functions. In S. L. Tsohatzidis (Ed.), *Intentional acts and institutional facts: Essays on John Searle's social ontology* (pp. 113–137). Berlin, Germany: Springer Verlag.

Rakoczy, H., Tomasello, M., & Striano, T. (2004). Young children know that trying is not pretending—a test of the "behaving-as-if" construal of children's early concept of "pretense". *Developmental Psychology*, *40*, 388–399.

Rakoczy, H., Tomasello, M., & Striano, T. (2005). On tools and toys: How children learn to act on and pretend with "virgin" objects. *Developmental Science*, *8*, 57–73.

Rakoczy, H., Warneken, F., & Tomasello, M. (2008). The sources of normativity: Young children's awareness of the normative structure of games. *Developmental Psychology*, *44*, 875–881.

Rakover, S. S. (1990). *Metapsychology: Missing links in behavior, mind and science*. New York: Solomon/Paragon.

Ralls, K., Fiorelli, P., & Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Canadian Journal of Zoology*, *63*, 1050–1056.

Range, F., Horn, L., Bugnyar, T., Gajdon G. K., & Huber, L. (in press). Social observing behaviour in keas, dogs, and human children. *Animal Cognition*.

Range, F., & Huber, L. (2007). Attention span of common marmosets: Implications for social learning experiments. *Animal Behaviour*, *73*, 1033–1041.

Range, F., Virányi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology*, *17*, 868–872.

Rapaport, L. G., & Ruiz-Miranda, C. R. (2002). Tutoring in wild golden lion tamarins. *International Journal of Primatology*, *23*, 1063–1070.

Ratner, N., & Bruner, J. (1978). Games, social exchange and the acquisition of language. *Journal of Child Language*, *5*, 391–401.

Rauschecker, J. P., Tian, B., & Hauser, M. (1995). Processing of complex sounds in the macaque nonprimary auditory cortex. *Science*, *268*, 111–114.

Rawls, J. (1955). Two concepts of rules. *Philosophical Review*, *64*, 3–32.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: Acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, *65*, 519–530.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society of London, Series B*, *272*, 941–947.

Reddy, V. (2003). On being the object of attention: Implications for self–other consciousness. *Trends in Cognitive Sciences*, *7*, 397–402.

Reik, W. (2007). Stability and flexibility of epigenetic gene regulation in mammalian development. *Nature*, *447*, 425–432.

Rendall, D. (2005). Pitch (Fo) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry. *Journal of the Acoustical Society of America*, *117*, 944–955.

Rendall, D., & Di Fiore, A. (2007). Homoplasy, homology, and the perceived special status of behavior in evolution. *Journal of Human Evolution*, *52*, 504–521.

Rendall, D., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, *51*, 1007–1015.

Richards, W. (Ed.). (1988). *Natural computation*. Cambridge, MA: MIT Press.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

Ridley, M. (2003). *Nature via nurture: Genes, experience, and what makes us human*. New York: HarperCollins.

Riese, M. L. (1987). Longitudinal assessment of temperament from birth to 2 years: A comparison of full-term and preterm infants. *Infant Behavior and Development*, *10*, 347–363.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188–194.

Rogoff, B., Mistry, J., Goncu, A., Mosier, C., Chavajay, P., & Heath, S. (1993). Guided participation in cultural activity by toddlers and caregivers. *Monographs of the Society for Research in Child Development*, *58*, 1–179.

Roian-Egnor, S. E., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*, 649–654.

Roian-Egnor, S. E., & Hauser, M. D. (2006). Noise-induced vocal modulation in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, *68*, 1183–1190.

Rolls, E. T., & Deco, G. (2001). *Computational neuroscience of vision*. Oxford, UK: Oxford University Press.

Romanes, G. J. (1883). *Mental evolution in animals*. London: Kegan Paul, Trench & Co.

Rooney, N., & Bradshaw, J. (2002). An experimental study of the effects of play upon the dog–human relationship. *Applied Animal Behaviour Science*, *75*, 161–176.

Rooney, N., & Bradshaw, J. (2006). Social cognition in the domestic dog: Behaviour of spectators towards participants in interspecific games. *Animal Behaviour*, *72*, 343–352.

Rose, E., & Felton, W. (1955). Experimental histories of culture. *American Sociological Review*, *20*, 383–392.

Ross, H. S., & Lollis, S. P. (1987). Communication within infant social games. *Developmental Psychology*, *23*, 241–248.

Roush, R. S., & Snowdon, C. T. (1994). Ontogeny of food associated calls in cotton-top tamarins. *Animal Behaviour*, *47*, 263–273.

Roush, R. S., & Snowdon, C. T. (2000). Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology*, *106*, 673–690.

Roush, R. S., & Snowdon, C. T. (2001). Food transfers and the development of

feeding behaviour and food-associated vocalizations in cotton-top tamarins. *Ethology*, *107*, 415–429.

Rowe, N. (1996). *The pictorial guide to the living primates*. New York: Pogonias Press.

Rukstalis, M., Fite, J. E., & French, J. A. (2003). Social change affects vocal structure in a callitrichid primate (*Callithrix kuhlii*). *Ethology*, *109*, 327–340.

Rumbaugh, D. M. (Ed.). (1977). *Language learning by a chimpanzee: The LANA Project*. New York: Academic Press.

Russ, B. E., Lee, Y. S., & Cohen, Y. E. (2007). Neural and behavioral correlates of auditory categorization. *Hearing Research*, *229*, 204–212.

Russell, C. L., Bard, K. A., & Adamson, L. B. (1997). Social referencing by young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*, 185–191.

Russell, J. L., Braccini, S., Buehler, N., Kachin, M. J., Schapiro, S. J., & Hopkins, W. D. (2005). Chimpanzee (*Pan troglodytes*) intentional communication is not contingent upon food. *Animal Cognition*, *8*, 263–274.

Ryan, M. J. (2005). The evolution of behavior, and integrating it towards a complete and correct understanding of behavioral biology. *Journal of Animal Biology*, *55*, 419–439.

Sahlin, N.-E., & Persson, J. (1994). Epistemic risk: The significance of knowing what one does not know. In B. Brehmer & N.-E. Sahlin (Eds.), *Future risks and risk management* (pp. 37–62). Dordrecht, The Netherlands: Kluwer.

Sakura, O. (1989). Variability in contact calls between troops of Japanese macaques: A possible case of neutral evolution of animal culture. *Animal Behaviour*, *38*, 900–902.

Salganik, M. J., Dodds, P. S., & Watts, D. J. (2006). Experimental study of inequality and unpredictability in an artificial cultural market. *Science*, *311*, 854–856.

Santos, L. R., Sulkowski, G. M., Spaepen, G. M., & Hauser, M. D. (2002). Object individuation using property/kind information in rhesus macaques (*Macaca mulatta*). *Cognition*, *83*, 241–264.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol*. New York: Columbia University Press.

Savage-Rumbaugh, E. S. (1990). Language acquisition in nonhuman species: Implications for the innateness debate. *Developmental Psychobiology*, *23*, 599–620.

Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. M. (1993). *Language comprehension in ape and child*. (Monographs of the Society for Research in Child Development, No. 58.) Chicago: University of Chicago Press.

Savage-Rumbaugh, E. S., Shanker, S. G., & Taylor, T. J. (1998). *Apes, language and the human mind*. Oxford, UK: Oxford University Press.

Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J., & Leitner, T. (2002). Genetic Evidence for an East Asian origin of domestic dogs. *Science*, *298*, 1610–1613.

Schaffner, C. M., & Caine, N. G. (2000). The peacefulness of cooperatively breeding primates. In F. Aureli & F. B. De Waal (Eds.), *Natural conflict resolution* (pp. 155–169). Berkeley, CA: University of California Press.

Schöning, C., Humle, T., Möbius, Y., & McGrew, W. C. (2008) The nature of culture: Technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution*, *55*, 48–59.

Schotter, A., & Sopher, B. (2003). Social learning and coordination conventions in intergenerational games: An experimental study. *Journal of Political Economy*, *111*, 498–529.

Searle, J. (1969). *Speech acts: An essay on the philosophy of language*. Cambridge, MA: Cambridge University Press.

Searle, J. R. (1983). *Intentionality: An essay in the philosophy of mind*. Cambridge, UK: Cambridge University Press.

Searle, J. R. (1990). Collective intentions and actions. In P. Cohen, J. Morgan, & M. Pollack (Eds.), *Intentions in communication* (pp. 401–415). Cambridge, MA: MIT Press.

Searle, J. R. (1995). *The construction of social reality*. New York: Free Press.

Searle, J. R. (2005). What is an institution? *Journal of Institutional Economics*, *1*, 1–22.

Seuss, D. (1957). *How the grinch stole Christmas!* New York: Random House.

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*, 1640–1658.

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 249–273). Cambridge, UK: Cambridge University Press.

Seyfarth, R. M., & Cheney, D. L. (2003). Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences*, *1000*, 32–55.

Seyfarth, R. M., Cheney, D. L., & Bergman, T. J. (2005). Primate social cognition and the origins of language. *Trends in Cognitive Sciences*, *9*, 264–266.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*, 1070–1094.

Shafer, D. D. (1988). Handedness in gorillas. *The Gorilla Foundation*, *8*, 2–5.

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. Urbana, IL: University of Illinois.

Shillito, D. J., Shumaker, R. W., Gallup, G. G., Jr., & Beck, B. B. (2005). Understanding visual barriers: Evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Animal Behaviour*, *69*, 679–687.

Sidky, H. (2004). *Perspectives on culture. A critical introduction to theory in cultural anthropology*. Lebanon, IN: Pearson Prentice Hall.

Simon, H. (1955). A behavioral model of rational choice. *Quarterly Journal of Economics*, *69*, 99–118.

Simon, H. A. (1957). *Models of man*. New York: Wiley.

Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society*, *106*, 467–482.

Slabbert, J. M., & Rasa, O. A. E. (1997). Observational learning of an acquired maternal behaviour pattern by working dog pups: An alternative training method? *Applied Animal Behaviour Science*, *53*, 309–316.

Slade, A. (1987). A longitudinal study of maternal involvement and symbolic play during the toddler period. *Child Development*, *58*, 367–375.

Slocombe, K. E., & Zuberbühler, K. (2005a). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, *119*, 67–77.

Slocombe, K. E., & Zuberbühler, K. (2005b). Functionally referential communication in a chimpanzee. *Current Biology*, *15*, 1179–1784.

Smedslund, J. (1994). What kind of propositions are set forth in developmental research? Five case studies. *Human Development*, *37*, 280–292.

Smith, D. R. R., Patterson, R. D., Turner, R., Kawahara, H., & Irino, T. (2005). The

processing and perception of size information in speech sounds. *Journal of the Acoustical Society of America*, *117*, 305–318.

Snowdon, C. T. (2001a). From primate communication to human language. In F. B. M. de Waal (Ed.), *Tree of origin: What primate behavior can tell us about human social evolution* (pp. 193–227). Cambridge, MA: Harvard University Press.

Snowdon, C. T. (2001b). Social processes in communication and cognition in callitrichid monkeys: A review. *Animal Cognition*, *4*, 247–257.

Snowdon, C. T., & Boe, C. Y. (2003). Social communication about unpalatable foods in tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *117*, 142–148.

Snowdon, C. T., & de la Torre, S. (2002). Multiple environmental contexts and communication in pygmy marmosets (*Cebuella pygmaea*). *Journal of Comparative Psychology*, *116*, 182–188.

Snowdon, C. T., & Elowson, A. M. (1999). Pygmy marmosets modify call structure when paired. *Ethology*, *105*, 893–908.

Snowdon, C. T., Elowson, A. M., & Roush, R. S. (1997). Social influences on vocal development in New World primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 234–248). New York: Cambridge University Press.

Sodian, B. (1991). The development of deception in young children. *British Journal of Developmental Psychology*, *9*, 173–188.

Sommers, M. S., Moody, D. B., Prosen, C. A., & Stebbins, W. C. (1992). Formant frequency discrimination by Japanese macaques (*Macaca fuscata*). *Journal of the Acoustic Society of America*, *91*, 3499–3510.

Spence, M. J., & Freeman, M. S. (1996). Newborn infants prefer the maternal low-pass filtered voice, but not the maternal whispered voice. *Infant Behavior and Development*, *19*, 199–212.

Sperber, D., & Wilson, D. (1986). *Relevance: Communication and cognition*. Oxford, UK: Blackwell.

Stabler, E. P. (2004). Varieties of crossing dependencies: Structure dependence and mild context sensitivity. *Cognitive Science*, *28*, 699–720.

Steels, L. (1999). *The talking heads experiment*. Antwerpen, Belgium: Laboratorium.

Steiner, S. M. (1990). Handedness in chimpanzees. *Friends of Washoe*, *9*, 9–19.

Stoinski, T. S., & Whiten, A. (2003). Social learning by orangutans (*Pongo abelii* and *Pongo pygmaeus*) in a simulated food-processing task. *Journal of Comparative Psychology*, *117*, 272–282.

Stoinski, T. S., Wrate, J. L., Ure, N., & Whiten, A. (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology*, *115*, 272–281.

Stout, D. (2002). Skill and cognition in stone tool production: An ethnographic case from Irian Jaya. *Current Anthropology*, *45*, 693–722.

Striedter, G. F. (2004). *Principles of brain evolution*. Sunderland, MA: Sinauer Associates.

Studdert-Kennedy, M. (2000). Evolutionary implications of the particulate principle: Imitation and the dissociation of phonetic form from semantic function. In C. Knight, M. Studdert-Kennedy, & J. R. Hurford (Eds.), *The evolutionary emergence of language: Social functions and the origins of linguistic form* (pp. 161–176). Cambridge, UK: Cambridge University Press.

Susswein, N., & Racine, T. (2008). Sharing mental states: Causal and definitional issues

in intersubjectivity. In J. Zlatev, T. P. Racine, C. Sinha, & E. Itkonen (Eds.), *The shared mind: Perspectives on intersubjectivity* (pp. 141–162). Amsterdam: Benjamins.

Sutcliffe, A. G., & Poole, T. B. (1984). Intragroup agonistic behavior in captive groups of the common marmoset *Callithrix jacchus jacchus*. *International Journal of Primatology*, *5*, 473–489.

Sutton, D., Larson, C., Taylor, E. M., & Lindeman, R. C. (1973). Vocalization in rhesus monkey: Conditionability. *Brain Research*, *52*, 225–231.

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, *62*, 591–598.

Szathmáry, E. (2001). Origin of the human language faculty: The language amoeba hypothesis. In J. Trabant & S. Ward (Eds.), *New essays on the origin of language* (pp. 55–81). Berlin, Germany: Mouton de Gruyter.

Taglialatela, J. P. (2007). Functional and structural asymmetries for auditory perception and vocal production in nonhuman primates. In W. D. Hopkins (Ed.), *Evolution of hemispheric specialization in primates* (pp. 117–142). Burlington, MA: Elsevier/Academic Press.

Taglialatela, J. P., Cantalupo, C., & Hopkins, W. D. (2006). Gesture handedness predicts asymmetry in the chimpanzee inferior frontal gyrus. *NeuroReport*, *17*, 923–927.

Taglialatela, J. P., Savage-Rumbaugh, E. S., & Baker, L. A. (2003). Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology*, *24*, 1–17.

Tanner, J. E., & Byrne, R. W. (1993). Concealing facial evidence of mood. Perspective taking in a captive gorilla. *Primates*, *34*, 451–457.

Tanner, J. E., & Byrne, R. W. (1996). Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology*, *37*, 162–173.

Temerlin, M. K. (1975). *Lucy: Growing up human*. Palo Alto, CA: Science and Behavior Books.

Terrace, H. S. (1979). *Nim*. New York: Knopf.

Teufel, C., Hammerschmidt, K., & Fischer, J. (2007). Lack of orienting asymmetries in Barbary macaques: Implications for studies of lateralized auditory processing. *Animal Behaviour*, *73*, 249–255.

Theall, L. A., & Povinelli, D. J. (1999). Do chimpanzees tailor their gestural signals to fit the attentional states of others? *Animal Cognition*, *2*, 207–214.

Thom, R. (1974). La linguistique, discipline morphologique exemplaire. *Critique*, *30*, 235–245.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*, 227–229.

Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433.

Tobler, I., & Sigg, H. (1986). Long-term motor activity recording of dogs and the effect of sleep deprivation. *Experientia*, *42*, 987–991.

Tollefsen, D. (2004). Collective intentionality. *The Internet encyclopedia of philosophy*. Retrieved 22 December 2005 from http://www.iep.utm.edu/c/coll-int.htm

Tomasello, M. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, P. G. Helthe (Eds.), *Chimpanzee cultures* (pp. 301–317). Cambridge, MA: Harvard University Press.

Tomasello, M. (1995a). Language is not an instinct. *Cognitive Development*, *10*, 131–156.

Tomasello, M. (1995b). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origin and role in development* (pp. 103–130). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 319–346). San Diego, CA: Academic Press, Inc.

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.

Tomasello, M. (2000). Primate cognition: Introduction to the issue. *Cognitive Science*, *24*, 351–361.

Tomasello, M. (2001). Cultural transmission: A view from chimpanzees and human infants. *Journal of Cross-Cultural Psychology*, *32*, 135–146.

Tomasello, M. (2003). The pragmatics of primate communication. In J. Verschueren, J. O. Östman, J. Blommaert, & C. Bulcaen (Eds.), *Handbook of pragmatics* (pp. 11–21). Amsterdam: Benjamins.

Tomasello, M. (2005a). Uniquely human cognition is a product of culture. In S. C. Levinson & P. Jaisson (Eds.), *The evolution of culture: A Fyssen Foundation Symposium* (pp. 203–218). Cambridge, MA: MIT Press.

Tomasello, M. (2005b). Comment on Everrett (2005). *Current Anthropology*, *46*, 640–641.

Tomasello, M. (2006). Why don't apes point? In N. Enfield & S. C. Levinson (Eds.), *The roots of human sociality: Culture, cognition and interaction* (pp. 506–524). Oxford, UK: Berg.

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states—the question is which ones and to what extent. *Trends in Cognitive Sciences*, *7*, 153–156.

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, *37*, 137–154.

Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M., & Nagell, K. (1997). The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication*, *1*, 223–259.

Tomasello, M., & Camaioni, L. (1997). A comparison of the gestural communication of apes and human infants. *Human Development*, *40*, 7–24.

Tomasello, M., & Carpenter, M. (2005). The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development*, *70*, 1–136.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*, 675–691; discussion 691–735.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. A. (1987). Observational learning of tool use by young chimpanzees. *Human Evolution*, *2*, 175–183.

Tomasello, M., George, B., Kruger, A., Farrar, M., & Evans, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution*, *14*, 175–186.

Tomasello, M., Gust, D., & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates*, *30*, 35–50.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, *16*, 495–552.

Tomasello, M., & Rakoczy, H. (2003). What makes human cognition unique? From individual to shared to collective intentionality. *Mind and Language*, *18*, 121–147.

Tomasello, M., & Zuberbühler, K. (2002). Primate vocal and gestural communication. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 293–299). Cambridge, MA: MIT Press.

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., et al. (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research*, *46*, 227–235.

Tonooka, R., Tomonaga, M., & Matsuzawa, T. (1997). Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees (*Pan troglodytes*). *Japanese Psychological Research*, *39*, 253–265.

Tooby, J., & Cosmides L. (1989). Adaptation versus phylogeny: The role of animal psychology in the study of behavior. *International Journal of Comparative Psychology*, *2*, 105–118.

Topál, J., Gácsi, M., Miklósi, Á., Virányi, Z., Kubinyi, E., & Csányi, V. (2005). The effect of domestication and socialization on attachment to human: A comparative study on hand reared wolves and differently socialized dog puppies. *Animal Behaviour*, *70*, 1367–1375.

Topál, J., Miklósi, Á., & Csányi, V. (1997). Dog–human relationship affects problem solving behavior in the dog. *Anthrozoös*, *10*, 214–224.

Topál, J., Miklósi, Á., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, *112*, 219–229.

Tramo, M. J. (2001). Music of the hemispheres. *Science*, *291*, 54–56.

Tramo, M. J., Bellew, B. F., & Hauser, M. D. (1996). Discharge patterns of auditory cortical neurons evoked by species-specific vocalizations and synthetic complex signals in alert *Macaca mulatta*. *Society for Neurosciences Abstracts*, *22*, 1623.

Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical applications. *Journal of Child Psychology and Psychiatry*, *42*, 3–48.

Tuomela, R. (1995). *The importance of us: A philosophical study of basic social notions*. Stanford, CA: Stanford University Press.

Tuomela, R., & Miller, K. (1988). We-intentions. *Philosophical Studies*, *53*, 367–389.

Ueno, A., & Matsuzawa, T. (2004). Food transfer between chimpanzee mothers and their infants. *Primates*, *45*, 231–239.

Vaid, J., Bellugi, U., & Poizner, H. (1989). Hand dominance for signing: Clues to brain lateralization. *Neuropsychologia*, *27*, 949–960.

Valsecchi, P., Choleris, E., Moles, A., Guo, C., & Mainardi, D. (1996). Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, *110*, 243–251.

Van de Walle, G. A., Carey, S., & Prevor, M. (2000). Bases for object individuation in infancy: Evidence from manual search. *Journal of Cognition and Development*, *1*, 249–280.

Van Lawick-Goodall, J. (1968). The behavior of free-living chimpanzees of the Gombe Stream Nature reserve. *Animal Behavior Monographs*, *1*, 161–311.

Van Parijs, S. M. (2003). Aquatic mating in pinnipeds: A review. *Aquatic Mammals*, *29*, 214–226.

Van Schaik, C. P. (2004). *Among orangutans: Red apes and the rise of human culture*. Cambridge, MA: Harvard University Press.

Van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C., Singleton, I., et al. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*, 102–105.

Van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution*, *36*, 719–741.

Varela, F., Thompson, E., & Rosch, E. (1991). *The embodied mind*. Cambridge, MA: MIT Press.

Vas, J., Topál, J., Péch, É., & Miklósi, Á. (2007). Measuring attention deficit and activity in dogs: A new application and validation of a human ADHD questionnaire. *Applied Animal Behaviour Science*, *103*, 105–117.

Vauclair, J. (1996). *Animal cognition: An introduction to modern comparative psychology*. London: Harvard University Press.

Vauclair, J. (2003). Would humans without language be apes? In J. Valsiner (Series Ed.) & A. Toomela (Ed.), *Cultural guidance in the development of the human mind: Vol. 7. Advances in child development within culturally structured environments* (pp. 9–26). Greenwich, CT: Ablex Publishing Corporation.

Vauclair, J. (2004). Lateralization of communicative signals in nonhuman primates and the hypothesis of the gestural origin of language. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*, *5*, 363–384.

Vauclair, J., Meguerditchian, A., & Hopkins, W. D. (2005). Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Research*, *25*, 210–216.

Vaughan van Hecke, A., Mundy, P., Acra, C. F., Block, J., Delgado, C., Parlade, M. V., et al. (2007). Infant joint attention, temperament, and social competence in preschool children. *Child Development*, *78*, 53–69.

Veà, J. J., & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica*, *69*, 289–290.

Vick, S. J., & Anderson, J. R. (2003). Use of human visual attention cues by olive baboons (*Papio anubis*) in a competitive task. *Journal of Comparative Psychology*, *117*, 209–216.

Vilá, C., Savolainen, P., Maldonado, J. E., Amorim, I. R., Rice, J. E., Honeycutt, R. L., et al. (1997). Multiple and ancient origins of the domestic dog. *Science*, *276*, 1687–1689.

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy D., & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves and dogs. *Animal Cognition*, *11*, 373–387.

Visalberghi, E. (1997). Success and understanding in cognitive tasks: A comparison between *Cebus apella* and *Pan troglodytes*. *International Journal of Primatology*, *18*, 811–830.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, *60*, 195–202.

Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE*, *2*(7), e611.

Von Uexküll, J. (1909). *Umwelt und Innenwelt der Tiere* [*Environment and inner world of animals*]. Berlin, Germany: Springer-Verlag.

Von Uexküll, J. (1940). *Bedeutungslehre* [*The study of meaning*] (Bios, Abhandlungen zur theoretischen Biologie und ihrer Geschichte sowie zur Philosophie der organischen Naturwissenschaften, Vol. 10). Leipzig, Germany: Barth.

Vygotsky, L. S. (1978). *Mind in society*. Cambridge, MA: Harvard University Press.

Waddington, C. H. (1957). *The strategy of the genes*. London, UK: Allen & Unwin.

Walton, K. L. (1990). *Mimesis as make-believe*. Cambridge, MA: Harvard University Press.

Wang, X., Merzenich, M. M., Beitel, R., & Schreiner, C. E. (1995). Representation of a species-specific vocalization in the primary auditory cortex of the common marmoset: Temporal and spectral characteristics. *Journal of Neurophysiology*, *74*, 2685–2706.

Warden, C., & Jackson, T. (1935). Imitative behaviour in the rhesus monkey. *Journal of Genetic Psychology*, *46*, 103–125.

Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development*, *77*, 640–663.

Washburn, S. L., & Benedict, B. (1979). Non-human primate culture. *Man*, *14*, 163–164.

Watanabe, K. (1994). Precultural behaviour of Japanese macaques: Longitudinal studies of the Koshima troops. In R. A. Gardner, B. T. Gardner, B. Chiarelli & F. X. Plooij (Eds.), *The ethological roots of culture* (pp. 81–94). Dordrecht, The Netherlands: Kluwer.

Waters, G., & Fouts, R. S. (2002). Sympathetic mouth movements accompanying fine motor movements in five captive chimpanzees (*Pan troglodytes*) with implications toward the evolution of language. *Neurological Research*, *24*, 174–180.

Weick, K. E., & Gilfillan, D. P. (1971). Fate of arbitrary traditions in a laboratory microculture. *Journal of Personality and Social Psychology*, *17*, 179–191.

Weiss, D. J., & Newport, E. (2006). Mechanisms underlying language acquisition: Benefits from a comparative approach. *Infancy*, *9*, 241–257.

Weissengruber, G. E., Forstenpointner, G., Peters, G., Kübber-Heiss, A., & Fitch, W. T. (2002). Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*), and domestic cat (*Felis silvestris* f. *catus*). *Journal of Anatomy* (London), *201*, 195–209.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: The truth about false belief. *Child Development*, *72*, 655–684.

Wellman, H. M., & Wooley, J. D. (1990). From simple desires to ordinary beliefs: The early development of everyday psychology. *Cognition*, *35*, 245–275.

Werdenich, D., & Huber, L. (2002). Social factors determine cooperation in marmosets. *Animal Behaviour*, *64*, 771–781.

Wernicke, K. (1874). *Der aphasische Symptomencomplex. Eine psychologische Studie auf anatomischer Basis* [*The aphasia symptom-complex: A psychological study on an anatomical basis*]. Breslau, Poland: Cohn & Weigert.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*, 477–508.

Whiten, A., & Custance, D. M. (1996). Studies of imitation in chimpanzees and children. In C. M. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 291–318). London: Academic Press.

Whiten, A., Custance, D. M., Gómez, J. C., Texidor, P., & Bard, K. A. (1996).

Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *110*, 3–14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in chimpanzees. *Nature*, *399*, 682–685.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*, 737–740.

Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning and Behavior*, *32*, 36–52.

Whiten, A., Horner, V., & Marshall-Pescini, S. (2003). Cultural panthropology. *Evolutionary Anthropology*, *12*, 92–105.

Wich, S. A., & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society: Biological Sciences*, *273*, 735–740.

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): An experimental study on male loud calls in response to a tiger model. *American Journal of Primatology*, *60*, 155–159.

Wildgen, W. (1982). *Catastrophe theoretic semantics: An elaboration and application of René Thom's theory*. Amsterdam: Benjamins.

Wildgen, W. (1994). *Process, image, and meanings. A realistic model of the meanings of sentences and narrative texts*. Amsterdam: Benjamins.

Wildgen, W. (1998). Chaos, fractals and dissipative structures in language: Or the end of linguistic structuralism. In G. Altmann & W. A. Koch (Eds.), *Systems, new paradigms for the human sciences* (pp. 596–620). Berlin: de Gruyter.

Wildgen, W. (2004). *The evolution of human languages: Scenarios, principles, and cultural dynamics*. Amsterdam: Benjamins.

Wildgen, W. (2005). Catastrophe theoretical models in semantics. In R. Köhler, G. Altmann, & G. Pietrowski (Eds.), *Quantitative linguistics: An international handbook* (pp. 410–423). Berlin: de Gruyter.

Wildgen, W. (2007a). Semiotic hypercycles driving the evolution of language. *Axiomathes*, *18*, 91–116.

Wildgen, W. (2007b). Evolutionary pragmatics. In J.-O. Östman & J. Verschueren in collaboration with E. Versluys (Eds.), *Handbook of pragmatics*. Amsterdam: Benjamins.

Wildgen, W. (2008). *Kognitive grammatik: Klassische paradigmen und neue perspektiven*. Berlin: de Gruyter.

Willatts, P. (1985). Adjustment of means–ends coordination and the representation of spatial relations in the production of search errors by infants. *British Journal of Developmental Psychology*, *3*, 259–272.

Willatts, P. (1999). Development of means–end behaviour in young infants: Pulling a support to retrieve a distant object. *Developmental Psychology*, *35*, 651–667.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, *13*, 103–128.

Wolf, M. E., & Goodale, M. A. (1987). Oral asymmetries during verbal and nonverbal movements of the mouth. *Neuropsychologia*, *25*, 375–396.

Wollberg, Z., & Newman, J. D. (1972). Auditory cortex of squirrel monkeys: Response properties of single cells to species-specific vocalizations. *Science*, *175*, 212–214.

Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee: The case of deception. *Cognition*, *7*, 333–362.

Worden, R. P. (1995). A speed limit for evolution. *Journal of Theoretical Biology*, *176*, 137–152.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, *16*, 97–159.

Xu, F., & Baker, A. (2005). Object individuation in 10-month-old infants using a simplified manual search method. *Journal of Cognition and Development*, *6*, 307–323.

Xu, F., & Carey, S. (1996). Infants' metaphysics: The case of numerical identity. *Cognitive Psychology*, *30*, 111–153.

Zuberbühler, K. (2000a). Causal cognition in a nonhuman primate: Field playback experiments with Diana monkeys. *Cognition*, *76*, 195–207.

Zuberbühler, K. (2000b). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, *59*, 209–220.

Zuberbühler, K. (2000c). Interspecific semantic communication in two forest monkeys. *Proceedings of the Royal Society, Biological Sciences*, *267*, 713–718.

Zuberbühler, K. (2000d). Referential labeling in Diana monkeys. *Animal Behaviour*, *59*, 917–927.

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli. Behavioral Ecology and Sociobiology*, *50*, 414–422.

Zuberbühler, K. (2003). Referential signaling in nonhuman primates: Cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*, *33*, 265–307.

Zuberbühler, K. (2005). The phylogenetic roots of language: Evidence from primate communication and cognition. *Psychological Science*, *14*, 126–130.

Zuberbühler, K. (2006). Language evolution: The origin of meaning in primates. *Current Biology*, *16*, 123–125.

Zuberbühler, K., Cheney, D. L., & Seyfarth, R. M. (1999). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, *113*, 33–42.

Zuberbühler, K., Noe, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour*, *53*, 589–604.

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