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Towards a bottom-up perspective on animal and human cognition

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Over the last few decades, comparative cognitive research has focused on the pinnacles of mental evolution, asking all-or-nothing questions such as which animals (if any) possess a theory of mind, culture, linguistic abilities, future planning, and so on. Research programs adopting this top-down perspective have often pitted one taxon against another, resulting in sharp dividing lines. Insight into the underlying mechanisms has lagged behind. A dramatic change in focus now seems to be under way, however, with increased appreciation that the basic building blocks of cognition might be shared across a wide range of species. We argue that this bottom-up perspective, which focuses on the constituent capacities underlying larger cognitive phenomena, is more in line with both neuroscience and evolutionary biology.

Introduction
A few decades ago, scientists focused on language – a typically human characteristic – to see how far apes could go with it. When attempts to teach apes speech failed, training moved to the gestural domain and performance exceeded expectations: symbolic communication seemed to be within the grasp of our close relatives [1]. Definitions of language were quickly changed, however, stressing syntax over reference [2].

The field of animal cognition rarely shies away from advanced faculties, leading to regular conflict regarding the human–animal divide. But what if we were to replace our obsession with complex cognition with an exploration of basic processes? Instead of asking which species can do X, the question would become how does X actually work? What are the necessary ingredients of X and how did these evolve? We pursue this bottom-up perspective in this article by reviewing recent research on future planning, imitation and altruistic behavior to demonstrate how complex capacities can often be broken down into components that humans share not just with the apes, but also with a host of other species. We argue that to document and understand these components at the neural level should be our highest priority. This approach, which has been gaining ground in the last few years, will move the field of comparative cognition towards an understanding of capacities in terms of underlying mechanisms and the

degree to which these mechanisms are either widespread or special adaptations.

From a top-down to a bottom-up approach
Even if continuity among all life forms is widely accepted in relation to anatomy, genetics, development and neuroscience, this view remains controversial when it comes to cognition. Proposals of discontinuity are innate in the top-down perspective that has steered comparative cognition in the direction of the most complex expressions of any given capacity. Do only humans have a theory of mind, or do apes, too? Can animals have culture? What is imitation and which species are capable of it? Do apes, in fact, ape? Does not reciprocal exchange require scorekeeping too demanding for any animal? Pitting humans against apes, apes against monkeys, primates against corvids, dogs against apes, and so on, it almost seems like a contest of 'who is the smartest of them all?' *Scala Naturae* assumptions remain prevalent enough that cognitive similarities between distant taxa, such as birds and primates, are sometimes viewed as antithetical to evolutionary theory [3].

The absence of certain cognitive abilities in certain taxonomic groups is critical to this approach, so negative evidence has received unwarranted attention. Although both positive and negative evidence risk being false, a profound asymmetry exists: there are many more possible reasons why an existing capacity might *not* be found than why a non-existing capacity could be found. This is why negative evidence should be treated with great circumspection. Nevertheless, failures to demonstrate certain capacities, along with premature conclusions about their absence, have appeared in major journals, such as the report that nonhuman primates do not care about the welfare of others [4], a claim contradicted by subsequent research (see the section on Prosocial behavior and empathy). Similarly, a failure to demonstrate that apes understand gravity has been taken to mean that only humans possess such an understanding [5], even though it would seem a rather adaptive capacity for arboreal primates, which do in fact show signs of this [6]. Debates around theory of mind and imitation have followed similar cycles of initial denial for nonhuman species based on negative evidence, with subsequent partial or complete acceptance based on experimental paradigms with greater ecological validity (see the section on Imitation).

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The result is a literature of claims and counter-claims regarding complex mental faculties with less of a focus on underlying mechanisms than on taxonomic dividing lines. Typical examples are the denial of imitation even in apes given that they fail to appreciate others as intentional agents [7], claims of '*humaniqueness*' (i.e. key differences between the cognition of humans and other animals) because animals lack the ability to combine old concepts into new ones [8], and the sweeping conclusion that 'the functional discontinuity between human and nonhuman minds pervades nearly every domain of cognition' [9,p. 110].

Others, however, have defended Darwin's view of mental continuity [10] or explained why cognitive similarity between distant species poses no problem for evolutionary theory. Tool use, for example, might have evolved independently to serve extractive foraging in the great apes, capuchin monkeys and New Caledonian crows. But even though a sound case for convergent evolution can be made [11], this does not necessarily imply independent neural mechanisms. The intriguing possibility exists of deep homologies in the cognitive domain, much as shared genetic instructions underlie the eyes or limbs of animals as distant as flies and rodents [12]. Re-evaluation of avian brain evolution has indicated that even though a layer-like organization is absent from the pallium, this structure might nevertheless derive from the same reptilian telencephalic structure as the mammalian neocortex [13]. If both structures accomplish similar functions, many avian and mammalian cognitive capacities could share homologous mechanisms.

The distinction between homology (i.e. shared ancestry) and analogy (i.e. independently evolved functional parallels) is less clear-cut in the cognitive domain than is often assumed [5]. Developed by anatomists, this distinction is easiest to apply to highly defined morphological and behavioral traits with a traceable phylogeny, such as fixed action patterns and facial expressions [14]. The same distinction is much harder to apply to traits that escape precise definition and measurement, such as cognitive capacities. Moreover, analogous traits often contain homologous elements in the same way that the wings of birds and bats are products of convergent evolution yet contain homologous bones. When shaping cognitive capacities, evolution often seems to act on behavioral predispositions and motivations while retaining core learning mechanisms [15]. Only if we know their genetic and/or neural underpinnings can capacities be confidently classified as either analogous or homologous. Recent research on face recognition in humans and other primates, for example, strongly suggests a shared neural background, and hence homology [16,17]. Until more such evidence is available, the most parsimonious Darwinian assumption is that if closely related species – whether they be squid and octopus or humans and apes – show similar solutions to similar problems, they probably involve similar cognitive mechanisms [18].

The overwhelming tendency outside of biology to give human cognition special treatment is commonly justified by pointing to our outsized cerebral cortex. The latest neuroanatomical evidence lends little support to this view, however, because our brain seems to be a linearly scaled-up primate brain [19]. Excessive attention to so-called higher cognitive functions and the corresponding neglect of subcortical processes in cognitive science have been criticized as 'corticocentric myopia' [20]. Some have gone so far as to label the fascination with uniquely human capacities as non-evolutionary, together with a warning against 'hopeful monsters', that is, the belief that a brief evolutionary time interval could have produced a well-integrated set of novel capacities [21]. Every species, including our own, comes with an enormous set of evolutionarily ancient components of cognition that we need to better understand before we can reasonably focus on what makes the cognition of each species special. Are cognitive specializations due to new capacities or rather to new combinations of old ones? Bottom-up approaches focus on these building blocks and represent a new *Zeitgeist* as reflected in the latest treatments of future planning [22], reciprocal altruism [23], theory of mind [24] and comparative cognition in general [25]. Another good example is the field of numerosity, which has moved from the all-or-nothing question 'Can animals count?' to a more diversified approach, noting how numerical skills are rooted in 'nonlinguistic biological primitives' [26].

Cognitive capacities are never all-or-nothing phenomena. Often they integrate a range of mechanisms and many species can be expected to show some but not all those underlying theory of mind, self-awareness, culture, language, reciprocal altruism, planning, and so on. An outcome-based science stresses differences, whereas a focus on process makes one wonder how deep these differences go and how outcomes are achieved. Theoretically, it is possible that different species achieve similar outcomes in different ways or use similar cognitive mechanisms to achieve different behavioral ends. Outcomes are important from an evolutionary perspective in that they determine an organism's success at dealing with its environment, but from a cognitive perspective they are mere surface phenomena. Unique outcomes do not always reflect unique processes. Even if humans produce cathedrals and symphonies, the underlying processes include social learning, tool use, musical appreciation, a sense of rhythm, and large-scale synchronization and cooperation, all of which we share with other animals.

The dissection of basic components of cognition, now more practicable with advanced technologies, aims to provide an understanding of how specific neural and behavioral mechanisms contribute to the organization of a given cognitive process and whether the same mechanisms operate across species. Mirror neurons are a case in point (Box 1). Unfortunately, however, entire books and treatises on animal intelligence barely mention neuroscience. With this in mind, we briefly review three areas of cognition research: memory and planning, imitation and prosocial behavior. Research in these areas is rapidly moving towards a bottom-up view in which mechanisms are central and species differences are less important.

Remembering the past and planning for the future

Remembering specific personal experiences has been considered a sign of autonoetic consciousness that is uniquely

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Box 1. Mirror neurons and the bottom-up approach

The mental life of animals is considered the result of their unique way of perceiving and integrating different types of sensory information into a single framework to form an internal representation. The merit of this cognitive approach has been in successfully comparing the sensory channels of different organisms and their psychophysical properties and in clarifying how the perceptual world is built and represented in an organism. However, this model of how organisms perceive the world rests on the idea that perceptual and motor functions are anatomically segregated in the brain. It also emphasizes the perceptual system as the core system for the analysis and representation of the external world. The discovery of neural mechanisms that combine action and perception, such as mirror neurons, has profoundly challenged this duality.

Mirror neurons were first found in the ventral premotor area F5 and subsequently in the inferior parietal lobe of macaques [27,28]. These neurons typically discharge both when a monkey performs a motor act (e.g. grasping an object) and when it observes the same, or a similar, act performed by an experimenter or another monkey. The possibility of matching the visual description of a goal-directed act with its cortical motor representation could allow extraction of important information about another's action, prompting the idea that these neurons could be involved in action understanding.

Using brain imaging and transcranial magnetic stimulation tools, several human studies demonstrated the presence of a mirror system involving the homolog premotor and parietal cortical areas [27], thus suggesting that this matching mechanism and its basic properties are a general part of primate brain evolution. Beyond coding the goal of motor acts, recent neurophysiology shows that mirror neurons also enable a monkey to discriminate between similar actions with different goals. It is possible that these neurons infer another's intentions, or *why* an individual does something [29].

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human [30] and includes the anticipation of future needs and drive states [31]. Other animals, it was claimed, use stored information merely to react to present stimuli or anticipate the immediate future.

Whereas autonoetic consciousness remains inaccessible in nonhuman animals, other aspects of the above claim have been challenged, starting with experiments on food-caching birds. Western scrub jays seem to have precise memories of past cashes, including the what, where and when characteristic of episodic memory [32]. Since then, human episodic memory has been dissected with more sophisticated tools by neuroscientists. Increasing evidence from neuroimaging and brain-damaged patients indicates that remembering past events involves regions of the hippocampus, parahippocampal gyrus and prefrontal cortex. Brain imaging shows that the same neural machinery that serves the recollection of autobiographical events is recruited to make plans, perhaps by piecing together memories of past events to simulate the future. Thus, episodic memory and planning rely on the same neural structures [33].

In this light, it is not surprising that the same birds said to possess episodic-like memory also seem capable of future planning, as reflected in storing food in anticipation of a future hunger state, as opposed to being affected by their current state [34]. The capacity to give future states priority over present preferences is also known for apes [35] (but see Ref. [36]). Even rodents can show some of these capacities. A recent neurophysiological study found activity in a specific cell assembly of the rat hippocampus during memory retrieval. The same assembly also predicts future choices, suggesting that rats, like humans, use a shared neural substrate for memory and action planning [37]. Therefore, instead of viewing episodic memory and future orientation as advanced language-mediated processes limited to humans, they should be considered as part of the general memory and action organization found to varying degrees in a wide range of species [22,38].

Imitation

Even though the population-specific traditions of wild primates are commonly attributed to social learning, primate imitation has become controversial ever since the classical definition of imitation as 'doing an act from seeing it done' [39] was replaced by a top-down definition requiring a subject to understand the intentional structure of another's actions, such as the other's goal and specific ways to achieve this goal [7,40]. Whereas apes and many other animals clearly exhibit imitation according to the old definition, the new definition has had the effect of excluding them (Box 2). Only humans have 'true' imitation, it was claimed.

However, the majority of studies failing to find ape imitation used human behavioral models. This is important in light of the increasing view of imitation in neuroscience that places less emphasis on perceived intentionality and more on the neural merging of perception and action as a result of body mapping between individuals. Given that body mapping relies on bodily correspondence and is probably enhanced by social closeness and identification, models of a different species than one's own are unlikely to be optimal. Negative results can be explained by this species barrier [41]. Once the extra effort had been made to train conspecific models, the issue of ape imitation was quickly settled to the point that major skeptics have come around to this view. Exposed to models of their own species, chimpanzees reliably and faithfully imitate tool use, foraging techniques and arbitrary action sequences [42–44].

This leaves the question of whether ape imitation is based on an actual understanding of the model's intentions. Even for human adults such understanding may not be essential [45], so simpler processes are likely. Imitation probably stems from internal or external mimicry of observed motor movements through shared neural representations [27,46]. Externally visible mimicry in chimpanzees is suggested by co-action, in which observers place their hand on the model's hand or tool, thus gaining kinesthetic feedback of the other's actions [44], or by observers that move an empty hand in precise synchrony with a nut-cracking companion 'consistent with a model of imitation in which the imitator codes its observation of the model immediately into a motoric representation' [47]. This would also explain why chimpanzees readily learn solutions to problems from each other but not from repeated demonstrations of the same solutions in the absence of a real-life companion [48]. Primate imitation depends on inter-individual action coding and not on perceived modifications of the physical environment.

Neuroimaging and neurophysiological studies in humans have shown that the cortical areas active during observation of another's actions are homologous with those containing mirror neurons in macaques [28,49]. These

Box 2. Do monkeys ape?

The role of mirror neurons in imitation is sometimes questioned because these neurons were discovered in monkeys, which lack imitation [52]. The latter statement is only true, however, if we narrowly define imitation in terms of another's understanding of another's intentions or of copying complex novel sequences. By any other standard, monkeys do have imitative skills. In the wild, they show socially learned cultural variation on a par with that of apes [53], and in the laboratory they reliably copy a conspecific's motor actions [54,55]. The tendency to do as others do is spontaneous, because monkeys require no rewards for it [56]. There is also evidence of neonatal imitation in monkeys [57] (Figure I) and an ability to recognize when they are *being* imitated [58]. In sum, if action coding is the essence of imitation, as argued here, monkeys most certainly qualify as imitators.

Figure I. Like human neonates, infant rhesus monkeys spontaneously mimic the mouth movements of a human experimenter suggesting the early presence of a neural mirroring system shared across species. Drawing by Frans de Waal from Ref. [57].

neurons are usually tested in relation to existing behavior, but can also mediate the acquisition of novel motor sequences. Humans show activation of the same neural areas of the mirror system during simple motor imitation, as during imitation of novel behavior, thus suggesting that copying of novel behavior recruits neural resources related to the existing action repertoire [50].

Now that mirror neurons have also been found in birds, it is assumed that the evolution of these neurons can be traced back to the common ancestor of birds and mammals [51]. Therefore, we should consider the theoretical possibility that *all* imitation has a shared neural perception–action foundation, from the vocal mimicry of birds to the copying of foraging techniques by primates. This would represent deep homology indeed.

Prosocial behavior and empathy

In the same way that the view of imitation went through a phase in which some of its manifestations were considered more true than others, research on prosocial behavior is commonly presented as a quest for 'true' altruism, defined as altruism without obvious advantages for the actor. From this perspective, aid to offspring or kin hardly qualifies (explained by kin selection) and any chance at reciprocation by the beneficiary also disqualifies altruism as genuine (explained by return benefits). But whereas these are critical distinctions in relation to the evolution of behavior, they hardly matter at the proximate level unless we assume that actors know about inclusive fitness and future returns. Thus far, there is no evidence that they do. Since one cannot want what one does not know about, altruistic motivations must stem from another source. Even animals capable of learning the advantages of reciprocity can only do so if they have a tendency to spontaneously help others in the first place [59].

We must therefore assume an altruistic impulse independent of incentives and long-term benefits. In one chimpanzee study, the role of incentives was manipulated. The apes spontaneously assisted humans and were also willing to assist conspecifics, without altering their behavior dependent on the availability of rewards [60]. Spontaneous helping has also been experimentally demonstrated in both marmosets [61] and capuchin monkeys [62,63]. In both human and nonhuman primates altruistic behavior correlates with socio-emotional connections between individuals, so the suggested motivational mechanism is empathy [59] (Figure 1). Empathy leads to a stake in another's welfare, so that helping comes with an intrinsic reward known in the human literature as the 'warm glow' effect. Humans report feeling good when they do good and show activation of reward-related brain areas [64].

Empathy might be widespread in mammals. It is thought to stem from an evolutionarily ancient perception–action mechanism, the most basic form of which is state matching, also known as emotional contagion [65].

Figure 1. Chimpanzees frequently react to another's need or distress with directed altruism. Here, a mother, having heard her son's screams, stretches out a hand to help him out of a tree. Recent experiments confirm that nonhuman primates care about the welfare of others, both kin and nonkin. Photograph by Frans de Waal.

This mechanism has been demonstrated in mice [66] and is being studied through yawn contagion in humans and other animals [67]. Like other forms of empathy, state matching occurs most readily among bonded individuals [66,68].

During observation of facial emotions, mirroring activation is present not only in human premotor areas, but also in insular and cingulate cortices [69,70]. These areas belong to neural circuits known for their involvement in visceromotor sensations related to unpleasant and painful stimuli. When we observe a facial expression, motorically similar expressions are unconsciously triggered, which are associated with corresponding emotions [71]. Thus, as with imitation, basic empathy runs from body to body rather than from mind to mind [72].

If empathy is indeed the main proximate mechanism of so-called directed altruism (i.e. altruistic behavior in response to another's distress or need [59]), the cognitively demanding assumption that acts of helping rest on cost–benefit analyses needs to be replaced with a socio-emotional perspective. Altruistic behavior unexplained by the first framework (e.g. humans sending money to distant victims of natural disasters) often does fit the second, a mechanism that might have evolved in social animals through individual selection rather than kin or group selection [73].

Concluding remarks

If there is one general trend in the field of comparative cognition, it is the rapid accumulation of evidence that more and more organisms show signs of any given capacity. In all areas discussed (i.e. episodic memory, planning, imitation and prosocial behavior), initial claims that humans, or at least hominoids, are special have had to be revised when related capacities were discovered in other, sometimes taxonomically quite distant, species. *De novo* appearances of cognitive capacities are apparently as unlikely as *de novo* anatomical features.

Rather than focus on the pinnacles of cognition, the field of comparative cognition seems to be moving towards a bottom-up perspective focused on the nuts and bolts of cognition, including underlying neural mechanisms (see Box 3). Most mechanisms are evolutionarily ancient, tying together phenomena such as bird song learning and the cultural acquisition of tool use in primates and the prosocial behavior of both humans and other mammals. This does not mean that distinctions between taxonomic groups are irrelevant or that there is no point to finer-grained classifications. But it does suggest that, instead of dividing imitation into one 'true' form and other forms – which apparently do not deserve the name – the most fruitful approach would be to return to the classical definition and include all forms of imitation in a single framework. Various forms of imitation can then be distinguished according to the function they serve in the lives of animals, the stimuli that determine their occurrence (i.e. body actions, perceived goals, changes produced in the environment) and the underlying cognitive processes as part of the even larger category of social learning. The same applies to empathy, which ranges all the way from automatic emotional activation in response to the behavior of others to perspective-taking that becomes increasingly complex with increasing brain size. The latter allows some species to gear their helping behavior specifically to another's situation and need. The most advanced forms of imitation and empathy are likely to encompass and build on more basic forms – and hence remain connected to the core mechanism – so our terminology should strive for conceptual unity rather than drive wedges between types.

In every given domain, functional refinements have evolved as adaptations to the ecology of a species, the study of which is critical for an evolutionary cognitive science. The most logical route for comparative cognition, however, is to try to understand the basic processes and common denominators first before exploring species-typical specializations.

> **Box 3. Specific outstanding questions raised by the bottom-up approach**
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> - Homology: if distantly related species evolve similar cognitive capacities to achieve similar ends (e.g. tool use in birds and primates) does this automatically mean that they use different neural mechanisms, or are their deep homologies in the neural components of their respective capacities?
> - Linking imitation and empathy: even though imitation and empathy manifest themselves in quite different behavior, to what degree do both rely on neural mechanisms of body mapping, action coding and shared representation, and is this reflected in correlations at the individual or species level between both capacities?
> - Mirror system: what is actually mirrored in the mirror system of humans and other primates, actions, intentions or motor goals? How do mirror neurons work in parallel or in conjunction with cognitive systems committed to inferential reasoning?
> - Inner templates: how does sensory and motor information converge during development to allow increasingly precise matching between the two? This is important in relation to early mirroring, such as neonatal imitation, in which matching occurs without visual experience. Are animals born with an internal template of their bodies, both their own and others?
> - Emotion recognition: a mirror-matching system concerning visceromotor reactions seems to be present within the human limbic system. Might this constitute an ancient mechanism – as old as the mammals, if not the vertebrates – for the automatic recognition of another's emotional state?

References

1 Gardner, R.A. and Gardner, B.T. (1969) Teaching sign language to a chimpanzee. *Science* 165, 664–672
2 Terrace, H.S. (1979) *Nim*, Knopf
3 Bolhuis, J.J. and Wynne, C.D.L. (2009) Can evolution explain how minds work? *Nature.* 458, 832–833
4 Silk, J.B. *et al.* (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357–1359
5 Povinelli, D.J. (2000) *Folk Physics for Apes: The Chimpanzee's Theory of How the World Works*, Oxford University Press
6 Hauser, M.D. *et al.* (2001) What guides a search for food that has disappeared? Experiments on cotton-top tamarins. *J. Comp. Psychol.* 115, 140–151
7 Tomasello, M. (1999) *The Cultural Origins of Human Cognition*, Harvard University Press

8 Hauser, M.D. (2009) The possibility of impossible cultures. *Nature* 460, 190–196

9 Penn, D.C. and Povinelli, D.J. (2007) On the lack of evidence that non-human animals possess anything remotely resembling a "theory of mind". *Philos Trans. R. Soc. Lond. B Biol. Sci.* 362, 731–744

10 de Waal, F.B.M. (2009) Darwin's last laugh. *Nature* 460, 175

11 Emery, N.J. and Clayton, N.S. (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 306, 1903–1907

12 Shubin, N. *et al.* (2009) Deep homology and the origins of evolutionary novelty. *Nature* 457, 818–823

13 Jarvis, E.D. *et al.* (2005) Avian Brain Nomenclature Consortium. Avian brains and a new understanding of vertebrate brain evolution. *Nat. Rev. Neurosci.* 6, 151–159

14 Preuschoft, S. and van Hooff, J.A.R.A.M. (1995) Homologizing primate facial displays: a critical review of methods. *Folia Primatol.* 65, 121–137

15 Papini, M.R. (2002) Pattern and process in the evolution of learning. *Psychol. Rev.* 109, 186–201

16 Tsao, D.Y. *et al.* (2008) Comparing face patch systems in macaques and humans. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19514–19519

17 Parr, L.A. *et al.* (2009) Face processing in the chimpanzee brain. *Curr. Biol.* 19, 50–53

18 de Waal, F.B.M. (1999) Anthropomorphism and anthropodenial: consistency in our thinking about humans and other animals. *Philos. Top.* 27, 255–280

19 Herculano-Houzel, S. (2009) The human brain in numbers: A linearly scaled-up primate brain. *Front. Hum. Neurosci.* 3, 1–11

20 Parvizi, J. (2009) Corticocentric myopia: old bias in new cognitive sciences. *Trends Cogn. Sci.* 13, 354–359

21 Margoliash, D. and Nusbaum, H.C. (2009) Language: the perspective from organismal biology. *Trends Cogn. Sci.* 13, 505–510

22 Raby, C.R. and Clayton, N.S. (2009) Prospective cognition in animals. *Behav. Processes* 80, 314–324

23 Brosnan, S.F. and de Waal, F.B.M. (2002) A proximate perspective on reciprocal altruism. *Hum. Nat.* 13, 129–152

24 Call, J. and Tomasello, M. (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* 12, 187–192

25 Shettleworth, S.J. (2010) *Cognition, Evolution, and Behavior*, (2nd edn), Oxford University Press

26 Nieder, A. and Dehaene, S. (2009) Representation of number in the brain. *Annu. Rev. Neurosci.* 32, 185–208

27 Rizzolatti, G. and Craighero, L. (2004) The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192

28 Ferrari, P.F. *et al.* (2009) From monkey mirror neurons to mirror-related behaviours: possible direct and indirect pathways. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 2311–2323

29 Fogassi, L. *et al.* (2005) Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667

30 Tulving, E. (2005) Episodic memory and autonoesis: uniquely human? In *The Missing Link in Cognition: Origins of Self-Reflective Consciousness* (Terrace, H.S. and Metcalfe, J., eds), pp. 3–56, Oxford University Press

31 Suddendorf, T. and Corballis, M. (1997) Mental time travel and the evolution of the human mind. *Genet. Soc. Gen. Psychol. Monogr.* 123, 133–167

32 Clayton, N.S. *et al.* (2003) Can animals recall the past and plan for the future? *Nat. Rev. Neurosci.* 4, 685–691

33 Schacter, D.L. *et al.* (2007) Remembering the past to imagine the future: the prospective brain. *Nat. Rev. Neurosci.* 8, 657–661

34 Correia, S.P.C. *et al.* (2007) Western scrub-jays anticipate future needs independently of their current motivational state. *Curr. Biol.* 17, 856–861

35 Osvath, M. and Osvath, H. (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim. Cogn.* 11, 661–674

36 Suddendorf, T. *et al.* (2009) How great is great ape foresight? *Anim. Cogn.* 12, 751–754

37 Pastalkova, E. *et al.* (2008) Internally generated cell assembly sequences in the rat hippocampus. *Science* 321, 1322–1327

38 Crystal, J.D. (2009) Elements of episodic-like memory in animal models. *Behav. Processes* 80, 269–277

39 Thorndike, E.L. (1898) Animal intelligence: an experimental study of the associate processes in animals. *Psychol. Rev. Monogr. Suppl.* 2, 551–553

40 Whiten, A. and Ham, R. (1992) On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In *Advances in the Study of Behavior* (Vol. 21) (Slater, J.B. *et al.*, eds), In pp. 239–283, Academic Press

41 de Waal, F.B.M. (2001) *The Ape and the Sushi Master*, Basic Books

42 Whiten, A. *et al.* (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437, 737–740

43 Bonnie, K.E. *et al.* (2006) Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proc. R. Soc. Lond. B Biol. Sci.* 274, 367–372

44 Horner, V. and de Waal, F.B.M. (2009) Controlled studies of chimpanzee cultural transmission. *Prog. Brain Res.* 178, 3–15

45 Horowitz, A.C. (2003) Do humans ape? Or do apes human? Imitation and intention in humans (*Homo sapiens*) and other animals. *J. Comp. Psychol.* 117, 325–336

46 Decety, J. and Chaminade, T. (2003) When the self represents the other: a new cognitive neuroscience view on psychological identification. *Conscious Cogn.* 12, 577–596

47 Marshall-Pescini, S. and Whiten, A. (2008) Social learning of nut-cracking behavior in East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *J. Comp. Psychol.* 122, 186–194

48 Hopper, L. *et al.* (2007) Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim. Behav.* 73, 1021–1032

49 Iacoboni, M. (2005) Neural mechanisms of imitation. *Curr. Opin. Neurobiol.* 15, 632–637

50 Iacoboni, M. (2009) Imitation, empathy, and mirror neurons. *Annu. Rev. Psychol.* 60, 653–670

51 Prather, J.F. *et al.* (2008) Precise auditory–vocal mirroring in neurons for learned vocal communication. *Nature* 451, 305–310

52 Visalberghi, E. and Fragaszy, D.M. (1990) Do monkeys ape? In *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (Parker, S. and Gibson, K., eds), pp. 247–273, Cambridge University Press

53 Perry, S. *et al.* (2003) Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate. *Curr. Anthropol.* 44, 241–268

54 Voelkl, B. and Huber, L. (2007) Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* 2 (7), e611

55 Dindo, M. *et al.* (2010) Conditional copying fidelity in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 124, 29–37

56 Bonnie, K.E. and de Waal, F.B.M. (2007) Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Anim. Cogn.* 10, 283–292

57 Ferrari, P.F. *et al.* (2006) Neonatal imitation in rhesus macaques. *PLoS Biol.* 4, e302

58 Paukner, A. *et al.* (2009) Capuchin monkeys display affiliation toward humans who imitate them. *Science* 325, 880–883

59 de Waal, F.B.M. (2008) Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* 59, 279–300

60 Warneken, F. *et al.* (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biol.* 5, e184

61 Burkart, J.M. *et al.* (2007) Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19762–19766

62 de Waal, F.B.M. *et al.* (2008) Giving is self-rewarding for monkeys. *Proc. Natl. Acad. Sci. U. S. A.* 105, 13685–13689

63 Lakshminarayanan, V.R. and Santos, L.R. (2008) Capuchin monkeys are sensitive to others' welfare. *Curr. Biol.* 18, R999–R1000

64 Harbaugh, W.T. *et al.* (2007) Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science* 316, 1622–1625

65 Preston, S.D. and de Waal, F.B.M. (2002) Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–72

66 Langford, D.J. *et al.* (2006) Social modulation of pain as evidence for empathy in mice. *Science* 312, 1967–1970

67 Campbell, M.W. *et al.* (2009) Computer animations stimulate contagious yawning in chimpanzees. *Proc. R. Soc. Lond. B Biol. Sci.* 276, 4255–4259

68 Palagi, E. *et al.* (2009) Contagious yawning in gelada baboons as a possible expression of empathy. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19262–19267

69 Wicker, B. *et al.* (2003) Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron* 40, 655–664

70 Singer, T. *et al.* (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303, 1157–1162

71 Dimberg, U. *et al.* (2000) Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11, 86–89

72 Niedenthal, P.M. (2007) Embodying emotion. *Science* 316, 1002–1005

73 Akçay, E. *et al.* (2009) A theory for the evolution of other-regard integrating proximate and ultimate perspectives. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19061–19066