



# Customs and cultures in animals and humans

Neurobiological and evolutionary  
considerations

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## Abstract

Anthropologists have long considered culture to be a defining attribute of humanity. Over the last decade, however, primatologists have repeatedly asserted that great apes also possess culture. Whether or not great apes or other animals pass the 'culture test' depends on how one defines culture. This article uses the terms 'custom' and 'symbolic culture' to distinguish socially transmitted behavioral patterns and symbolic systems of belief, each of which is sometimes called culture. Information presented here indicates that social customs are widespread among mammals. It remains questionable, however, whether any non-human animals possess symbolic cultures. Symbolism, teaching, imitation, speech, and gesture demand brain-size mediated neurological capacities possessed by few non-human species. These include fine motor skills and the ability to construct variable, complex motor acts, concepts, and objects from multiple components. Humans exceed all other animals in these mental constructional skills and, hence, in many abilities that rely upon them including language, making complex tools, art, dance, mime, teaching and imitation. These interacting capacities enhance our social learning abilities and also allow us to create and transmit symbolic systems of belief. Symbolic cultures, thus, may be creations of social beings equipped with prerequisite motor and mental capacities, and they may reflect activities of multiple neurological areas as opposed to being a discrete human trait mediated by a specific, genetically-determined neural module. To the extent that symbolic cultures are creations, all mental capacities essential for culture may have been present in ancestral humans prior to the appearance of actual evidence of culture in the archaeological record.

## Key Words

brain • culture • human evolution • mammals • primates • social learning

Humans display many behaviors that, depending on the perspectives of individual scholars, may or may not be considered cultural, and that, in toto, contribute to a

distinctly human way of life. These include, among others, language, dance, music, ritual, mime, sports, art, technology, social rules and laws, dietary and other customs, and systems of belief. Humans exhibit individual and collective creativity in each of these domains, and they transmit their creations and other information through social channels thereby creating group differences in customs and beliefs. From the standpoint of human evolution, key questions revolve around whether culture is also present in other animals and, if not, how and why it evolved in humans. Biological anthropologists also question the neurological foundations of human cultural capacities. For example, is culture simply a by-product of human neural plasticity, does it reflect a specific neural module dedicated to generating culture, or does it emerge from the interactions of other human cognitive and motor capacities?

Scholars who attempt to address these issues are often stymied by the diverse uses of the term, culture. Tylor (1871) defined culture as 'that complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society'. During the 20th century, however, anthropological concepts of culture experienced many perturbations. Some scholars excluded overt behaviors from culture which they defined as systems of abstractions, ideas and symbols that govern behavior (Beals and Hoijer, 1953; Kroeber and Kluckhohn, 1952). According to White (1959), culture is a 'class of things and events dependent upon symboling, considered in extrasomatic contexts'. In other words, in White's view, culture is a system of relationships among symbolized things and events: e.g. the symbolic relationships between concepts such as mother-in-law taboos, forms of marriage, and place of residence after marriage, rather than the individual customs per se. In contrast, other anthropologists continue to include behaviors that may distinguish groups of individuals from each other and that are learned and transmitted in a social context within the concept of culture (see Cronk, 1999: 132–3 for a list of varied definitions of culture). Many modern Americans would claim that population differences in behaviors, such as whether one uses chop-sticks or knives and forks, prefers pasta to potatoes, takes mid-day siestas, or practices polygyny, are cultural differences. Such population differences in behavioral customs do not qualify as culture, if culture is defined as abstractions, ideas or symbolic systems, but they do qualify as culture with respect to Tylor's definition and with respect to definitions that emphasize population differences in socially learned and transmitted behaviors.

Culture, according to Kroeber and Kluckhohn (1952), is 'that which the human species has and other social species lack'. Similarly, 'Man and culture originated simultaneously; this by definition' (White, 1959). Whether or not culture is truly unique to the human species, however, may depend on how one defines culture. This article examines questions of human and animal culture and its cognitive and neurological bases in the light of comparative mammalian behavioral data. In order to accommodate discrepant views of culture as symbolic systems versus culture as socially learned and transmitted behavioral patterns, social customs are distinguished from symbolic cultures. By custom, I mean socially, rather than genetically, transmitted behavioral patterns that may lead to behavioral differences between social groups of the same species. By symbolic culture, I mean symbolic systems of values and beliefs that may govern behavioral practices. Evidence reviewed in this article indicates that many mammalian species have social customs, as defined here, but none have yet been demonstrated to possess symbolic

culture. Although several primatologists have stated that chimpanzees and great apes or other primates possess culture, these claims rest on definitions of culture as socially-learned behaviors, rather than as symbolic systems (Boesch, 2000; de Waal, 2001; Kummer, 1971; McGrew, 1992; McGrew and Tutin, 1978; Russon, 2000; Whiten et al., 1999; Wrangham et al., 1994).

Comparative neurological, behavioral, and genetic evidence presented here suggests that human symbolic culture is unlikely to rest primarily on neural plasticity, which appears to be widespread in mammals, or to represent specific selection for a 'culture' neural module. Rather, individual human cultural capacities reflect the expansion and interaction of numerous brain regions and mental capacities. Indeed, symbolic cultures may naturally emerge from social interactions among humans equipped with other mental capacities such as language, tool-making, and advanced motor and social learning skills. That culture may emerge suggests that mental capacities necessary for culture may have appeared in pre-modern humans prior to actual evidence of culture in the archaeological record. Similarly, given the ability of great apes and some other highly intelligent species to use, and even invent, symbols, the possibility that a few non-human species might possess symbolic cultures or at least the capacities for such cultures cannot be entirely ruled out.

### **SOCIAL CUSTOMS IN NON-PRIMATE MAMMALS**

The individual discovery of survival-promoting behavioral patterns, through trial and error or other means, can be a lengthy, uncertain, and potentially risky process, in that many animals might die prior to acquiring efficient behavioral strategies. Genetic transmission of behaviors can assure that, under normal conditions, animals will develop behaviors that were adaptive in ancestral situations, but it cannot provide the behavioral flexibility necessary to survive in changing environments. It is also potentially costly in terms of DNA. Hence, in relatively stable environmental situations in which similar survival strategies can be used over relatively long periods of time, those young animals capable of quickly and effectively learning from their elders would be expected to be favored by natural selection (Boyd and Richerson, 1988; Laland et al., 1993). Similarly, in rapidly fluctuating environments, selection would favor those individuals capable of readily learning new foraging, travel, and other strategies from their peers. The ability to learn from peers may also have survival advantages for relatively opportunistic species that search for large patches of food that, once found, can nourish large numbers of animals. In other words, theoretical considerations suggest that social learning should be widespread among animals.

The extent, however, to which animals can actually learn from conspecifics, depends upon several factors including the species sensorimotor and learning capacities, group social structure, and species life history patterns. Acquired behavior patterns can be transmitted in both vertical and horizontal directions (Laland et al., 1993). Vertical transmission primarily refers to the transmission of information or skills from adults to immature animals, although, in some species, transmission may also occur in the opposite direction from the young to their elders. Horizontal transmission refers to social transmission among adults or peers. All mammals are exposed to maternal influences *in utero* and during periods of postnatal suckling. All young mammals, therefore, can potentially acquire information and behavioral practices from their mothers provided

they have the requisite sensorimotor and learning capacities. In some mammals, such as canids and marmosets, the young may also be cared for by adult males, and many rodents, ungulates, elephants, and whales live in large herds or social groups. Such settings provide opportunities for social transmission of acquired information and skills from varied adults to the young and vice versa. In group-living animals, these opportunities may continue in the post-weaning period, and group-living animals also have opportunities to transmit information among adults or peers.

From a life history perspective, the young of species that mature slowly over a period of years will have a greater length of time to acquire information from adults prior to maturity. In long-lived species, the population elders may also possess knowledge of survival-promoting reactions to rare environmental events which, depending on the species' mental capacities, can be socially transmitted should these events recur.

Mounting evidence indicates that mammals of diverse species take advantage of the social learning opportunities available to them. In particular, the social transmission of survival-promoting *information* pertaining to diet, predators, and migratory patterns is especially common in mammals and can lead to alterations in behavioral patterns (Box and Gibson, 1999). The social transmission of *skills and motor procedures* is less common, but is found in some mammals.

In many mammals, the social transmission of dietary information begins *in utero* or during the suckling period. In species that consume plant foods, such as marsupials, rabbits, sheep, and humans, dietary information is often transmitted via chemicals that cross the placental barrier or are present in maternal milk (Broom, 1999; Hudson et al., 1999). For example, at six months of age, the offspring of human mothers who drank carrot juice while pregnant or lactating preferred carrot-flavored porridge to water-flavored porridge. Other infants failed to express such preferences (Holden, 2000). In many species, the capacity to transmit food preferences *in utero* or through maternal milk may well have survival advantages by priming the young to prefer nourishing, non-poisonous dietary resources. In humans and in other species with diverse diets, it may also help channel infantile food choices in the directions preferred by local populations (Holden, 2000).

During the suckling period, the young of nestling species, such as rats and rabbits, also acquire maternal or group dietary preferences via the feces and breath of returning foragers (Hudson et al., 1999; Wilkinson and Boughman, 1999). Adult carnivores with altricial young, such as felids and canids, introduce their offspring to preferred parental foods by regurgitating partially digested food and/or by bringing dead or partially immobilized prey to the den or other nesting site (Kitchener, 1999; Nel, 1999). The young of mobile mammals, such as ungulates, whales, elephants, and juvenile felids and canids, acquire dietary preferences by following group members and foraging on the same foods that they do.

Some of the best examples of horizontal transmission have been found in rodents. In laboratory settings, it is possible to induce specific food preferences or dislikes in individual rats by standard reinforcement techniques. When these rats return to their group setting, other rats acquire feeding cues from their breath and feces and begin to preferentially forage on and/or avoid the same foods (Galef and Wigmore, 1983). By these means, experimenters have been able to create populations of laboratory rats with specific dietary preferences. Transmission chain studies that remove trained rats from the

groups and replace them with naive rats indicate that experimenter-reinforced food traditions continue to be transmitted within a group long after the removal of the initially trained animals (Laland, 1999). Similar mechanisms of social-transmission of food preferences are used by other group-living opportunistic feeders, such as naked mole rats and bats (Faulkes, 1999; Hudson et al., 1999).

Any species that socially transmits dietary preferences has the potential to develop population and group variations in dietary customs. The extent to which population dietary differences exist exclusive of those necessitated by the environmental availability of dietary resources has not been investigated for most species, but is known in some instances. Some otter populations, for example, forage on shellfish; others do not. Some orca (killer whales) forage primarily on fish; others prefer sea lions (Boran and Heimlich, 1999). A family of bears in Yellowstone National Park that socially transmitted a habit of feeding on human camp food was exterminated and removed because of danger to humans (Gilbert, 1999).

The social acquisition of distinct foraging techniques, such as specific hunting or food processing techniques, appears to be much less common in mammals than is the social acquisition of dietary preferences, but there are some reported cases. One population of black rats in Israel has developed a population-specific foraging technique of pine-cone stripping not known in other black rat populations (Terkel, 1996). Laboratory experiments indicate that these rats learn their stripping techniques by manipulating pinecones that have been partially stripped by other rats, an indirect, but in this instance a highly effective means, of socially transmitting a group-specific foraging procedure. Young elephants also manipulate tough plant foods that have already been partially processed by adults and may learn foraging techniques in this manner.

Many adult felids and canids provide their young with what has been termed 'opportunity learning' sessions by bringing dead or live prey to the nesting area (Caro and Hauser, 1992). This permits the young to practice dismemberment and killing techniques. Such practices may accelerate the maturation of hunting skills and, hence, the acquisition of independence. In most cases, these practices primarily hone, refine, and appropriately direct species-specific hunting techniques, rather than lead to the transmission of population-specific, novel hunting procedures. A few instances of the social transmission of novel hunting procedures have been well documented in felids, however (Kitchener, 1999).

Possibly the most dramatic instances of population-specific, socially transmitted, foraging techniques can be found in cetaceans (Boran and Heimlich, 1999). In order to capture sea lions from beaches, orca in the Puget Sound region must beach themselves. In doing so, they run the risk of becoming permanently stranded. Adult whales watch and sometimes demonstrate as young whales practice beaching and sea lion capture techniques. Similar socially transmitted beaching techniques have been reported for populations of dolphins. Some dolphin populations also exhibit population-specific customs of using tools to extract buried fish and of working together with human fishermen to herd fish into nets. Humpback whales create bubble nets to entrap schools of fish. Group-specific forms of bubble nets have been created and socially transmitted (Janik, 1999).

In addition to providing some of the clearest evidence for socially transmitted foraging techniques, cetaceans provide the best mammalian evidence for the social transmission

of another form of motor learning – learned vocalizations (Janik, 1999). Sea-living mammals, including whales, dolphins, and, possibly, sea lions, can create and imitate novel vocal utterances. Dolphins, for instance, create whistle signatures that serve to identify individual dolphins, and male humpbacked whales create group songs each breeding season. Other individuals may copy an individual dolphin's signature whistle, and the humpback breeding songs are modified by groups of whales practicing song variants together. The result of cetacean vocal capacities is that some species, such as orca, exhibit vocal dialects in different populations.

### **SOCIAL CUSTOMS IN NON-HUMAN PRIMATES**

Monkeys and apes tend to have long life spans as well as long gestational and maturational periods. Hence, they have opportunities for vertical transmission of behavioral patterns over lengthy periods of time. In all species, these opportunities exist between mother and young. In species with paternal care of offspring, in monogamous species, and in species that live in one-male groups, opportunity also exists for social transmission between fathers and young. Non-human primate group sizes vary considerably with the result that some species experience much greater opportunities for horizontal transmission of behavioral patterns and/or for vertical transmission from non-parental adults than do others. Baboons, for example, live in large groups, while gibbon groups consist primarily of a male–female pair and their offspring. Great apes appear to exceed monkeys in their social learning abilities (Gibson, 1999), and they also have longer life spans and longer periods of maturation. They do not, however, necessarily experience greater opportunities for the horizontal or vertical transmission of behavioral patterns. Gorillas, for instance, live in small one-male groups, and orangutans, at some stages in their lives, are largely solitary except for very small groups of a single mother with her immature offspring.

Distinct, socially transmitted, tool-using and other food processing techniques are found among populations of wild primates. One of the earliest and best known of primate food-processing traditions is that of the sweet potato and rice washing population of Japanese macaques. In the 1950s, a young female macaque began washing potatoes in the sea, presumably to remove grit, but possibly also to season the food with salt (Kawai, 1965). Within a few years, most members of the troop were also washing their potatoes, and many were washing rice. Although these are among the most dramatic of the reported cases of social transmission of food-processing procedures in monkeys, they required only minimal mastery of new motor skills. Sweet potato washing, in particular, seems to have required only the acquisition of the habit of carrying food to water. Although less famous, the baboon practice of foraging on underground corms may actually require more motor skills. King has noted that young baboons learn to acquire and process these food resources in a social setting, in part, by observing what others eat and where they acquire their food and, in part, by manipulating food already partially processed by other animals (King, 1994, 1999). It is not clear, however, whether there are population differences in corm processing techniques.

McGrew (1992), Boesch (2000), Russon (2000) and others have documented population differences in dietary preferences in chimpanzees and other great apes that are clearly independent of local food availability. In addition, great ape populations of the same species sometimes differ in their preferred food processing techniques. For example

chimpanzee nut-cracking, termiting, and anting techniques vary between groups (Boesch, 2000; McGrew, 1992). Some chimpanzee populations have tool-using techniques that take years to learn and may even be difficult for humans to master. In part, these complex techniques are learned by watching others use tools and, in part, by much motor practice. In two observed instances, a chimpanzee mother demonstrated a tool-using technique to one of her offspring (Boesch, 1993). Similarly, the feeding techniques of primarily herbivorous gorillas are surprisingly complex and involve socially transmitted step-wise procedures of folding and processing foods in order to avoid nettle stings and other noxious structures (Byrne, 1995, 1999). Finally, as noted by Russon (2000), orangutan extractive foraging strategies often require a series of complex manipulations, learned, in part, by observations of others.

These population variations in great ape tool-using techniques qualify as social customs. It is also tempting to call them culture. Indeed, many scholars do (Boesch, 2000; de Waal, 2001; McGrew, 1992; Russon, 2000; Whiten et al., 1999; Wrangham et al., 1994). However, they do not meet the definitions of culture used in this article, because they involve no symbolism.

In the non-dietary realm, chimpanzees use varied communication patterns in different populations. Chimpanzees of the Mahale Mountains of western Tanzania have invented a new social custom, not present in other chimpanzee groups: the grooming hand-clasp (McGrew et al., 2000). As delineated by Boesch (2000), other chimpanzee populations have invented leaf-clipping and knuckle-knocking displays that they use to communicate specific meanings such as intent to play or to engage in courtship. These behaviors are of great interest because the invention of novel gestures by non-human animals has rarely been described. In addition, to the extent that some of these behaviors, notably leaf clipping and knuckle-knocking, have specific communicative meanings not obvious from the communicative form, they may be considered symbolic. That wild apes can create symbolic gestures suggests the possibility that they might possess rudimentary symbolic cultures, that is, cultures based upon ideas and symbolic systems. To date, however, no evidence has emerged of the existence of symbolic cultures in great apes.

## **SOCIAL CUSTOMS AND SYMBOLIC CULTURES IN HUMANS**

Many human population differences in diet, tool-use, speech, gesture and other behavioral patterns may primarily qualify as social customs rather than as symbolic culture. Indeed, humans appear to exceed all other animals in the extent to which they have developed population-specific social customs. Humans have the longest life spans and the longest gestation and maturation periods of all primates. They also habitually live in populations containing both male and female adults and a number of children. Hence, they would appear to have the greatest opportunities for both vertical and horizontal transmission of behavioral patterns of all primate species. These circumstances no doubt greatly contribute to the diversity of human customs. It is important to note, however, that opportunities for the social transmission of novel behavior patterns vary greatly with time and place depending on life span and population size, and they are probably much greater in modern industrial and post-industrial societies than ever before in human history.

Human social customs span the range of mammalian social customs and include

population differences in dietary preferences, foraging techniques, vocal traditions, gestural communication patterns, and tool-using techniques. Humans also appear to exceed most other mammals in their abilities to develop at least two interrelated types of social customs: those that involve tool-making and those that involve the invention and transmission of novel motor patterns. Human tool-using and tool-making skills have been the focus of much literature (Gibson and Ingold, 1993). Much less emphasis has been placed on other motor learning skills possessed by our species. Great apes, especially orangutans, must learn complex techniques of moving through trees, and chimpanzees, orangutans, and gorillas master complex food manipulation techniques. Humans fall short of great apes in their arboreal locomotor capacities. Humans, however, invent and socially transmit motor rituals, dance, gymnastic and sport routines, and motor routines essential to extremely diverse forms of tool use and tool making, such as playing a violin, weaving cloth, and lassoing a bull. Humans also exceed all other primates in their ability to create novel vocal sequences.

Human abilities to master motor and tool-using customs render human culture dependent upon human custom, because humans communicate their thoughts via motor and/or tool-using channels. Symbolic language, for example, is communicated via learned vocal, gestural, or written motor routines that are acquired in a social context and conform to socially agreed upon conventions. Depiction and symbolic art also require motor routines and usually demand artistic media and tools.

Indeed, the ability to create and transmit learned motor and tool-using patterns is so critical to human symbolic communication that, in some cases, the extent to which human–ape differences in language reflect cognitive or symbolic capacities versus motor capacities is unclear. Some orangutans, gorillas, chimpanzees, and bonobos have managed to learn and use language-like symbols, but none have learned to express symbols through the vocal channel, although some can clearly comprehend many English words and some English grammar (see articles in Gibson and Ingold, 1993 and in Parker and Gibson, 1990). Some great apes can communicate rudimentary symbolic thought via gestural channels, but the most successful ape-language experiments have required that the apes do nothing more than point to visual symbols.

Human customs and culture are inextricably intertwined in other respects as well. Human symbolic capacities can be used to transmit and reinforce customs as well as to endow customs with symbolic status that they might not originally have had.

## **THE NEURAL AND MENTAL FOUNDATIONS OF SOCIAL CUSTOMS AND SYMBOLIC CULTURES**

For an animal species to manifest social customs, its members must possess the ability to learn individually and from conspecifics. They must also possess the neural plasticity that makes learning possible. They do not, however, need to be highly intelligent, since very simple perceptual mechanisms such as the detection of chemicals in feces or breast milk can be used to transmit information.

Learning ability has been demonstrated in many invertebrate species and across a very wide range of vertebrates. Similarly, social learning (learning from conspecifics) has been found in goldfish, birds, and a wide range of mammals including marsupials, carnivores, herbivores, cetaceans, ungulates, elephants, rodents, bats, and non-human primates (articles in Box and Gibson, 1999). Neural plasticity is also widespread in mammals in



all age groups. The brains of rats, equivalent in age to 80-year-old humans, for instance, increase in size in relationship to environmental enrichment (Diamond, 1988). The neocortices of adult rats can also form new synapses, and it now appears that adult rats, humans, and birds generate new neurons in the hippocampus – a subcortical neural structure involved in the formation of new memories (Mishkin et al., 1984). Adult monkeys, whose fingers have been ablated or whose arms have been kept in splints, experience neocortical functional reorganization with the result that the neural representations for other fingers or limbs enlarge (Merzenich and Kaas, 1982). These considerations suggest that the learning skills and neural plasticity essential to the development of social customs are widespread in animals, especially mammals.

Humans, of course, also possess learning ability and neural plasticity. These capacities contribute to the human abilities to create and transmit social customs and cultures. Learning capacities similar to those found in most mammals, however, cannot by themselves account for human culture or for human abilities to create complex motor and technological customs that cannot be created by other animals. Rather, humans appear to possess enhanced learning capacities and other mental capacities that are less universal among mammals.

In particular, human culture, language, motor and technical customs depend not only on our abilities to understand complex factual information and abstractions, they also depend on our ability to execute learned motor actions in a rapid and automatic way. This latter form of learning is called procedural learning (Mishkin et al., 1984). Procedural skills are mastered through much practice. Once mastered, however, they can be performed automatically with little conscious thought. Learned procedures can be very simple automatic acts, such as always pressing the brake when the light turns red. Alternatively, they can involve the routine activation of complex motor or 'intellectual' sequences: e.g. automatically eliciting a speech sequence, automatically using appropriate grammar, and/or reciting the alphabet or counting to ten without having to stop and think about the next letter/number in the sequence. Procedural learning coupled with motor and mental constructional skills (see next paragraph) allows humans to make and use complex tools, to draw, to write, to dance, and to engage in various rituals and athletic routines.

It has also been suggested elsewhere that a particular mental process, hierarchical mental construction, subserves human motor and cognitive abilities including symbolic and syntactic capacities, imitative capacities, and social intelligence (Gibson, 1990, 1996; Gibson and Jessee, 1999). By hierarchical mental construction is meant the fractionation of perceptions, actions, or ideas into fine component parts, the recombination of these fractionated units into new motor, sensory, and conceptual constructs, and the ability to embed new constructs into still higher order constructs. For example, humans can make extremely fine movements of the tongue and lips. They can combine individual movements of these and other oral structures into different oral postures in order to make specific phonetic sounds. They then string these sounds together to make words which, in turn, can be embedded into phrases, which can be embedded into sentences and so on. Similarly, motor hierarchical construction skills mediate dance, gymnastics, typing, and other complex motor routines. Humans, but not wild apes, also construct tools by manufacturing individual tool components that are then joined together with other components to make a constructed tool: e.g. manufacturing spear

points, shafts, and binding materials and binding them together into a higher order construct.

Mental construction is also evident in human social intelligence and language capacities. Dennett (1988), for example, talks about theory of mind as exhibiting different degrees of embeddedness. Contrast, for instance, the following sentences. John likes Mary. John thinks that Mary likes him. Mary thinks that John thinks that she likes him. Each of these progressively more complex sentences exhibits greater degrees of mental construction and embeddedness as well as greater abilities to consider the thought processes of others. Capacities to comprehend the thinking processes of others are essential for teaching. Imitative learning of new motor skills also requires mental construction because it demands the ability to compare perceptions of one's own actions with those of other individuals. Finally, detailed analyses of the development of human syntactic, symbolic, and other cognitive capacities emphasize their mental constructional foundations (Case, 1985).

It is important to recognize that the mental abilities that allow humans to combine various perceptions, actions and concepts into more complex constructions also underlie our creativity. We can combine units in flexible, highly varied ways, and, thus, can create novel and unique constructs. Our mental constructional skills in combination with our learning, especially procedural learning, abilities and our neural plasticity allow us to create new customs, rituals, symbols, rules, and belief systems and to transmit these creations via teaching, language, demonstration, and imitation.

Mental constructional abilities are also present in other animals, but to a lesser degree (Gibson, 1990). Given, for example, their abilities to invent novel motor techniques and to demonstrate techniques to each other, it is possible that some cetaceans, such as orca, dolphins, and humpbacked whales, have well-developed mental and motor constructional skills. Great apes also exhibit hierarchical mental constructional techniques in their tool-making and other complex foraging techniques, in ape-language experiments, and in imitative and teaching domains (Byrne, 1995; Byrne and Russon, 1998), but they fall far short of humans in the complexity of their mental constructions in several realms. Great apes, for instance, can use individual gestural and pictorial symbols in a language-like way and combine them into two-unit syntactic utterances (Greenfield and Savage-Rumbaugh, 1990), but they do not construct the complex hierarchical sentences that humans construct (Gibson and Jessee, 1999). They do make tools, but they do not construct them from diverse previously constructed components. Apes do have advanced motor abilities, but they fall short of humans in their abilities to create novel dance, mimetic, and tool-using motor routines. They do imitate (Byrne and Russon, 1998). However, when imitating a complex series of actions on objects, they seem to imitate only the end result of each object manipulation step, not the actual motor actions involved.

Elsewhere it has been argued that, in animals, enhanced mental and motor constructional skills require enlarged brains (Gibson, 1990). For example, cetaceans, who appear to exceed most mammals in mental constructional abilities, also have enlarged brains. Human-like mental constructional skills reflect not only overall brain size increases, but also enlargement of those regions of the brain that mediate motor skills, procedural learning, language, and tool-making including the neocortex, basal ganglia, cerebellum, and limbic system (Gibson and Jessee, 1999). To the extent that culture and custom

depend on mental construction, they, too, would reflect these increases in size of neural structures. From this perspective, it is important to note that great apes, who appear to have greater mental constructional capacities than do monkeys, also have larger brains, neocortices, basal ganglia, limbic systems, and cerebellums.

The mental constructional perspective presented here contrasts with the perspectives of those evolutionary psychologists who suggest that a different genetically-determined neural module underlies most distinguishable human intellectual capacities, such as language and social intelligence (Barkow et al., 1992; Pinker, 1994). Rather, mental construction is seen as a general ability common to all higher intellectual capacities and mediated by widely interacting portions of the brain. The mental constructional model has several advantages over the models of evolutionary psychologists in that it is compatible with existing knowledge of limited genetic differences between great apes and humans and of human and ape abilities to acquire new cultural behaviors that were not part of their evolutionary environment. The mental constructional model also has distinct implications for the nature of the human evolutionary environment. Specifically, it suggests that humans and perhaps great apes evolved to meet the demands of highly variable environments, rather than in a specific environment of evolutionary adaptation (see also, Potts, 1996).

## THE EVOLUTION OF HUMAN CULTURAL CAPACITIES

A synthesis of the neural and cognitive evidence, thus, suggests the following model. The common ancestor of monkeys and apes possessed the neural plasticity and learning capabilities characteristic of mammals in general. In early anthropoids, these abilities would primarily have been manifested in visual, tactile, and manual modes in keeping with their sensorimotor adaptations. In comparison to monkeys, the common ancestor of the great apes and hominids possessed overall brain enlargement as well as enlargement of those neural regions known to play a major role in motor learning and mental construction. Hence, ancestral ape-hominid abilities to create customs, especially motor customs, were somewhat greater than those of monkeys. Human evolution witnessed major brain size expansion coupled with major expansion in hierarchical mental and motor constructional techniques – hence, enhanced abilities to create and transmit customs and symbolic cultures and to execute complex, learned behavioral routines automatically and rapidly.

Throughout human history and prehistory, mental constructional skills interacted with neural plasticity to create and change human customs and cultures. As culture and custom changed in material, artistic, linguistic, social, and other directions, maturing and adult human brains experienced changing environmental inputs. As successive generations applied their mental constructional skills to these changing environmental inputs, they created novel customs and beliefs unlike those created by predecessors with different experiences. These processes had the predictable result of cultural 'evolution.' The same processes of application of mental constructional capacities to differing environmental inputs also help explain why apes reared in captivity display human-like abilities, such as language and enhanced tool-making, that they appear not to display in the wild. In both hominids and great apes, however, the rate of change in customs and cultures would likely have varied with population size and life span. Larger populations contain larger numbers of individuals to create new behavior patterns and beliefs. Also,

the larger the population and the greater the life span, the greater the chances of transmitting novel customs and beliefs to others and of having them survive within the population.

Current evidence indicates that the rudiments of most human cognitive and motor capacities are present in great apes and, hence, would have been present in the common ancestor of great apes and hominids (Gibson, 1991, 1996; Gibson and Jessee, 1999). The first clear evidence for hominid advances in mental constructional techniques over those exhibited by great apes is the manufacture of Acheulian hand-axes beginning about 1.5 million years ago and continuing to about 200,000 years ago. By this point in time, the genus, *Homo*, had appeared and brain sizes were about twice as large as those of the average great ape. The creation of hand-axes requires more steps and more planning than the manufacture of earlier flake tools, hence, more mental construction. The making of a specific tool form for over a million years also clearly indicates the presence of well-developed imitative skills by that time period (Mithen, 1999). Some argue that the manufacture of the same tool over a lengthy period of time indicates stereotyped thinking patterns. This tool, however, appears to have been the Swiss Army knife for early members of our genus – capable of being used to fell and dismember game, hurl at predators, dig, and process plant food. Mental flexibility during these earlier times, thus, may have been more evident in the use of tools in varied ways, than in the use of varied manufacturing techniques. These early groups would also have experienced sparse population densities and short life spans, hence, minimal opportunities for the invention, social transmission, and social preservation of new technologies.

During the Mousterian period approximately 200,000 years ago to about 30,000 years ago, some population variations in tool-making techniques existed, and tools were being constructed by joining two or more components together. Both Neanderthals and the earliest anatomically modern humans manufactured and used Mousterian tool-kits (Lieberman and Shea, 1994). Both had brains of at least modern size and, as best it can be determined from endocasts, of modern form. The presence of modern brains and constructed tools would argue for the presence of modern intelligence and modern capacities for the creations of customs and cultures in both Neanderthals and early modern humans (Gibson, 1996).

Little evidence of art or other symbolic activities survives from the Mousterian period. Nor did Mousterian peoples create a wide range of finely crafted tools. This contrasts strongly with the major flowering of art and fine tool-making that characterized upper Paleolithic peoples beginning about 40,000 years ago, i.e. beginning 70,000 or more years after the appearance of fully modern humans. This evidence is often interpreted to mean that language and symbolic culture evolved only with the onset of the upper Paleolithic. It is sometimes interpreted to mean that modern humans experienced major changes in brain function about 50,000 years ago even though no change in brain size or form has been documented for that time period (Klein, 1992). How can one explain the existence of modern human brains that lacked modern human mental capacities? Moreover, sporadic art works have been found from periods prior to the upper Paleolithic (Marshack, 1989), and some upper-Paleolithic-like tools were produced in Africa more than 100,000 years ago (Brooks et al., 1995).

If all factors known to contribute to the emergence of social customs and symbolic cultures are considered, possible explanations of these phenomena emerge other than

lack of symbolic and cultural capacities in Neanderthals and early modern humans. First, the European upper Paleolithic was accompanied by major population expansions, hence, increased numbers of individuals to create, transmit, receive, and preserve novel customs. Second, most archaeological evidence of social customs and symbolic activities derives from the remains of material cultures and other practices that demand tool-use, e.g. burial practices and art. Symbolic language and ritual could have existed prior to the invention of essential tools for symbolic art. Cave art, in particular, required torches or lamps, ladders or other means of reaching high places, a variety of extracted pigments and means of applying them. Bead-work requires the means of creating precise holes and polishing surfaces, and it requires string or fine cordage. The creation of such objects also requires time and implies a population with sufficient food procurement technology to liberate individuals from subsistence activities in order to pursue art. The nature of technology is also that each new technological advance builds upon its predecessors. Hence, a major technological explosion could only have occurred subsequent to the establishment of a more rudimentary technological foundation.

Given these considerations, it is perhaps to be expected that rates of technological change were very slow among the earliest members of our genus and species and are now sometimes overwhelmingly rapid. No new cognitive or symbolic abilities need be postulated to account for sudden rapid rates of change in custom and culture at any time since the emergence of modern human brain size and structure.

#### **WHY DID THE CAPACITY TO CREATE SOCIAL CUSTOMS AND CULTURE EVOLVE? – A FEW THOUGHTS**

Many human social customs involve survival-enhancing strategies such as diet and technology. We know that humans exploit foods, such as large game and underground tubers, that are not exploited by great apes, that they inhabit a wider range of climates and habitats than do other primates, and that the exploitation of diverse habitats demands diverse technologies and diverse dietary practices. Our ability to devise and socially transmit new environmental strategies clearly enhances our adaptive diversity and is likely to have been selected for in that context. Our needs to manipulate more complex tools and to be physically flexible when hunting large game may also, in part, explain the selective pressures that led to our increased motor combinatorial capacities and procedural learning skills.

Given, however, that other animals have the abilities to create new social customs, one must ask what selective advantages are provided by human symbolic culture as opposed to human social customs? Some of our survival-enhancing customs are transmitted linguistically, as is information about social and environmental resources. Hence, our symbolic abilities also appear to enhance our ability to exploit diverse environments. Ritual and dance can be used to transmit information about past and current events, and they help cement social bonds. Hence, they also appear to have potential survival advantages. Dance and music, however, can contribute to social bonding even when not of a symbolic nature. Similarly, pantomime and scene re-enactment can transmit information without symbolism. Perhaps, however, symbolism enhances communication by providing shared systems of understanding that allow for briefer explanations. Symbolism, especially in the form of ritual and belief in supernatural powers, also seems especially adept at reinforcing social rules and values that enhance group cohesion and

survival as opposed to selfish individualism. Possibly, then, symbolic cultures were selected for in hunting populations or in adverse environments that required group survival strategies, hence, increased group cohesion.

Alternatively, to play devil's advocate, perhaps symbolic cultures, per se, were never really selected for. Perhaps, cultures are mere creations of a species that evolved language, tool-use and advanced motor skills for survival-enhancing reasons and learned to use these skills to create symbolic systems.

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