

many-body dynamics on appropriate energy landscapes, similar to the physics concept of spin glasses. S. A. Kauffman (1993), for example, characterized evolutionary dynamics as adaptive walks on rugged fitness landscapes and correlated the statistics of these landscapes (in terms of quantities such as average numbers of local peaks, average distance between peaks, and correlations between fitnesses at fixed distances on the landscape) with the effectiveness of evolution on these landscapes. Other researchers have built on Motoo Kimura's (1983) idea of selective neutrality and applied statistical physics concepts such as percolation to characterize evolutionary dynamics on neutral networks. Others still have adapted concepts and methods from statistical mechanics and advanced statistics to describe population dynamics in simple evolutionary systems at a coarse-grained level. For example, E. van Nimwegen and colleagues (1997, 1999) have used such methods to demonstrate that metastable behavior in evolutionary systems can be the result of finite-population effects and can in some simple simulated cases be predicted in detail, and have proposed that these and related results may explain emergent behaviors seen in molecular evolution.

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— MELANIE MITCHELL AND MARK NEWMAN

CONSCIOUSNESS

There is no consensus on the correct concept of consciousness, or even whether it is unitary construct. Hence, a discussion of its evolution is difficult and controversial. It may be possible, however, to determine which living taxa have specific capacities related to consciousness, and then make the best cladistic inference as to the timing of the appearance of these capacities. A number of types or features of consciousness are widely recognized. For example, many scholars accept a distinction between *experiences* and *thoughts*.

Experiences are usually acknowledged as having evolved earlier than thought and are often considered to be prerequisite for thought. To have an experience is, as Thomas Nagel (1984) put it, for there to be some way "that it is like" to be in that state. The capacity for experience may have evolved quite early, as minimal forms of this capacity may include the ability to experience pain or experience stimulation of sense receptors. But it is extremely difficult to determine which organisms have experiences of any specific type. For example, no simple behavioral criteria would reliably indicate the presence of pain. Some single-celled organisms will move away from (or be attracted by) certain types of stimuli, but the ability to discriminate among (behave differentially in response to) different stimuli does not guarantee a conscious experience. Planaria, for example, will reliably retreat from light sources, but most scholars would not wish to attribute to them the experience of pain.

In contrast to experience, conscious thought is more abstract and requires concepts. Highly flexible, context-

dependent responses have been taken by some researchers as an indicator of the presence of thought. And at least some degree of flexibility of response is present in most organisms with full-blown perceptual organs. Certainly, behavioral evidence for categorization, problem solving, and "concept formation" has been accumulated in laboratory studies of various species of birds and mammals, and especially nonhuman primates. Whether the mental processes underlying such behaviors are "conscious thought," however, is controversial and difficult to establish.

The division between experience and thought is a psychologically important one, but it cuts across what many, if not most, would consider to be the essential feature of consciousness, namely reflective self-consciousness—what Thomas Natsoulas (1985) brands "Consciousness 4." Many scholars would happily grant consciousness of objects to those species with sensory systems that are capable of detecting and responding to those objects in the first place. They would further allow that these creatures are aware of something (and, in some cases, aware of a great deal) about their environment, and that some of these species may even possess concepts of such objects and think about them. Nonetheless, many of these same scholars would not grant that these organisms are conscious in the sense of being aware of their own mental states. This self-reflective component may be a crucial difference between humans and other animals. According to this view, humans—and only humans—not only perceive objects and feel hungry, but also know that they perceive and feel.

This form of self-knowledge is distinct from, though possibly dependent upon, knowledge of oneself as a distinct object in the environment (i.e., a minimal ability to explicitly represent and think about one's body as distinct from other objects). Implicit knowledge of one's body must be widespread among animals and would have evolved very early on—possibly as early as the evolution of full-blown sense organs. But this would not count as evidence for the type of reflective consciousness under discussion. Instead, Consciousness 4 is a type of *second-order mental state*—a representation of a mental state—and in this case, a representation of one's own mental state.

The evolution of reflective consciousness is controversial (see Gallup, 1998, and Povinelli, 1998, for a brief recap of the controversy). The central issues concern the nature of the self-concept in our closest living relatives, chimpanzees, and further, whether they are aware that they (or others) have mental states.

The most popular view is that chimpanzees in particular, and perhaps other species as well, possess a robust self-concept—representing to themselves their own bodies and mental states, as well as representing the mental

states of others. Although part of this view is based upon experimental evidence, much of it appears to derive from the degree of similarity in the spontaneous social behavior of humans and other species. For example, many species, especially among social primates, practice forms of behavioral deception. Because we believe we are reasoning about the mental states of others when we deceive them, we assume that roughly the same thing happens in other species who practice deception.

However, both parts of the popular view may be false. With respect to the question of a self-concept, the most widely cited argument in favor of reflexive consciousness in chimpanzees comes from their well-demonstrated ability to recognize themselves in mirrors. Gallup (1998) and others have shown that chimpanzees and orangutans (but not other primates) use mirrors to explore their own bodies. Further, if their ears or eyebrow ridges are surreptitiously marked with a red mark, and they are then allowed to interact with a mirror, they will reach up and explore these marks on their own bodies (see, e.g., Gallup, 1998), whereas other nonhuman primates presented with the same task touch the mirror. Gallup has interpreted these behaviors as evidence of a robust self-concept in chimpanzees and orangutans (and its absence in other species). He has further suggested that chimpanzees and orangutans may therefore be capable of introspection, and as such, capable of using their own internal mental states to model or simulate the mental states of others.

Others have suggested alternatives to this interpretation of self-recognition in mirrors (see, e.g., Povinelli, 1998). First, passing the mirror test of self-recognition may indicate only that an organism appreciates the equivalence between what they see in the mirror and what is happening with their own body, not a recognition that they see *themselves* per se (see Povinelli, 1998). Although this would imply that chimpanzees and orangutans, unlike most other primates, may possess at least an on-line, explicit, and usable representation of the kinesthetic aspects of their bodies, it need not imply that they possess a reflective awareness of mental states (such as emotions, desires, or beliefs). One potential evolutionary account of why great apes and humans may possess a more explicit and integrated representation of their bodies than other primates has been proposed by Povinelli and Cant (1995). Their "clambering hypothesis" begins by noting that the common ancestor of the great apes and humans quadrupled in body size over a 10–20 million year period, but were forced to remain almost exclusively arboreal. Using the "clambering" behavior of modern orangutans as a rough model, they demonstrated that these two factors (body size and extreme arboreality) would have created severe difficulties for these animals in translocating their bodies

across the gaps in the canopies, and therefore would have created strong selection pressures for a self-representational system dedicated to planning movements and their effects upon the environment. This evolutionary increase in body size—unprecedented in other highly arboreal primate groups—might have left a psychological imprint on the great ape/human lineage: a more explicit representation of the body and its movements.

Some researchers have attempted to assess more directly whether animals are aware of their own mental states. These “meta-memory” tasks generally involve conditional discrimination problems in which, on certain very difficult trials, the animals are given the option not to make a choice and instead advance to the next, possibly easier, trial (e.g., Smith, Shields, Washburn, and Allendoerfer, 1998; Hampton, 2001). Although intriguing, the amount and type of pretraining involved in such tasks make it unclear whether the responses involve conscious recollection and assessment (as opposed to implicit knowledge). Further, it seems quite possible that the animals are making assessments of their own behavior (as opposed to their mental states).

With respect to the question of whether chimpanzees or other species are aware of (or represent) the mental states of others, there is growing reason to be cautious. Consider something as seemingly simple as realizing that others have visual experiences—that is, understanding that they “see” things. Aspects of the behavior of chimpanzees, such as spontaneously following the gaze direction of others, would seem to suggest that they must appreciate that others “see.” However, demonstrating that chimpanzees make this simple inference about a perceptual state (i.e., “seeing”) has proven difficult, and further, there is a substantial body of carefully controlled, experimental evidence to suggest that they do not (see Povinelli, 2001). This stands in contrast to the ease with which this ability can be demonstrated in young children.

For some, this may seem biologically counter-intuitive. Why would similar behaviors in humans and other primates be attended by different kinds of awareness? For example, if humans follow the gaze of others in order to determine what they “see,” then why should we suppose that gaze-following in chimpanzees is triggered by different representations? A model that we have labeled the “reinterpretation hypothesis” reconciles the experimental and naturalistic evidence by arguing that many of the spontaneous behaviors that humans and chimpanzees share in common, behaviors which seem to be driven by an awareness of the mental states of others (e.g., gaze following, “cooperation,” “deceit,” reconciliation after fights), originally evolved under the control of psychological systems that represent the behavior, but not the mental states of others (see Povinelli

and Giambrone, in Povinelli, 2001). The model assumes that before there were any organisms on earth capable of reasoning about the mental states of others, many species already possessed complex nervous systems that were capable of detecting the various statistical regularities in the behavior of others. As the central nervous system initially diversified and enlarged, natural selection acted to favor variants that could detect and process the important regularities in the world of a given species, and in highly social species that would have included the regularities in the behavior of conspecifics with whom they must live and mate. The reinterpretation hypothesis postulates that the human lineage uniquely evolved an additional ability, not present in other primate species, which allowed us to interpret these already existing behaviors as being caused by internal psychological states. This new system (probably intimately related to human language) may have forever altered our commonsense interpretation of our own behavior and the behavior of those around us.

But if the fabric of human social behavior initially evolved without the operation of second-order intentional states, then what did second-order mental states add to human behavior? Put another way, what causal role do our second-order mental states play in generating our behavior? We have argued that this role may be complex. First, it is possible that second-order mental states may simply be rapid, after-the-fact explanations of behaviors that were actually prompted by other “unconscious” psychological systems. In other cases, although a given second-order mental state may be generated before the execution of a behavior, it may still play no causal role in generating it (although this temporal pattern may create the cognitive illusion that it did play such a role). Finally, in still other instances, the second-order mental state may occur prior to the behavior *and* play a causal role in launching a behavior. On this view, one of the main initial functions of second-order mental states was to modulate already existing behaviors, giving humans added flexibility in the timing and context of their deployment. The complex causal role that second-order mental states may play in human behavior is illustrated in Figure 1.

Two concluding points are in order. First, we have deliberately made no appeal to neuroscience to help determine the evolutionary history of various aspects of consciousness. Although some claim support for early emergence of consciousness on the basis of gross anatomical similarities or particular kinds of cortical organizations between human brains and those of various other animals, at this point we are reluctant to make any judgments on the basis of neurological similarities or differences. As Todd Preuss (2000) has emphatically noted, neuroscience has vigorously pursued investigating neurological similarities between humans and pri-

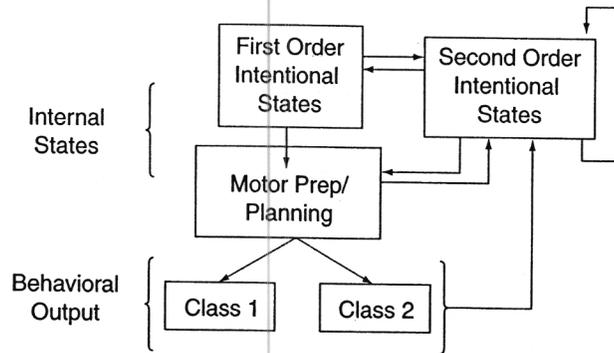


FIGURE 1. Complex Social Behaviors Shared by Humans and Chimpanzees.

The shared behaviors are directly generated by first-order intentional states, but in humans, second-order intentional states sometimes prompt the internal states that produce those behaviors. In many cases, humans may generate second-order intentional states after we have already begun (or completed) the very behaviors that our folk psychology uses them to explain. Second-order intentional states have initially evolved to simply play a role in regulating, organizing, and planning behaviors that were already present. The uniquely human aspects of this system are connected by the shaded arrows. Drawing by authors.

mates, but has placed far less emphasis on understanding the neural differences between humans and other primates. Indeed, so few resources have been expended investigating the unique aspects of human neurology that Francis Crick has described the situation as “scandalous.” The relatively few investigations of the differences between human brains and those of other primates have revealed very important dissimilarities, even areas where one would least expect to find such differences (e.g., primary visual cortex). Finally, from the opposite perspective, even if the human brain turned out to have numerous neural systems not found in our closest primate relatives, we know of no reasonable argument to support a claim that the same mental states, conscious or otherwise, must be underpinned by the same neurological states.

Finally, no evolutionary explanation of consciousness explains in any ultimate sense why experiences and *explicit* higher-order mental states (i.e., higher-order mental states that have some experiential feel to them) should exist as they do. The qualitative feel of mental states, as opposed to the information they bear, does not serve any obvious biological function. It could simply be an accident of evolutionary history on earth that there should be something “that it is like” to be in some mental states. But it could also be the case that internal states could not function as they do in humans without having a qualitative feel to them—although no one has, as of yet, offered any good reason for believing such a claim.

[See also Human Sociobiology and Behavior, *article on Evolutionary Psychology; Primates, article on Primate Societies and Social Life.*]

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sciousness, the first 5 chapters provide a thorough review of what is known about learning, concept formation, abstraction, and categorization in non-human primates.

— STEVE GIAMBRONE AND DANIEL J. POVINELLI

CONSENSUS TREES. See Phylogenetic Inference.

CONSTRAINT

Constraint implies a limitation to evolutionary change. Although very old, the concept has been revitalized in recent years as evolutionary biologists increasingly recognize that there are limits to adaptive evolution and that not all phenotypes are possible. Nonetheless, constraint remains a controversial topic and there is no consensus on exactly what it is or how to define it. This article first discusses some background concepts, then explores several classes of constraints operating on organisms.

In general, constraints are mechanisms or processes that inhibit the ability of the phenotype to evolve or bias its evolution along certain paths. The historical operation of constraints within a clade leads to evolutionary patterns, such as the unusually persistent stability of certain characters. Such patterns may initially suggest the action of constraint because they deviate from our expectation for how evolution would have proceeded in the *absence* of constraint. This expectation represents a "null model" for evolution against which the results of constraint can be compared. An alternative scenario is that the persistent stability of some characters reflects the action of natural selection, maintaining the character at some optimum.

Establishing a null model is a critical aspect of constraint theory; different null models lead to different notions of constraint. For molecular biologists interested in the evolution of DNA nucleotide sequences, for example, the null model of evolution is point substitution of nucleotides by random mutation. The expected pattern is random variation of nucleotide sequences among species. When a particular site or sequence is found to be invariable (it deviates from the null model), it is sometimes said to be "constrained," in this case meaning it is under stabilizing selection because a change in nucleotides would cause harmful functional effects in the proteins specified by the affected codon. In contrast, organismal biologists interested in phenotypic evolution most often use adaptive evolution by natural selection as their null model. The failure of the phenotype to evolve in response to selection is taken as evidence of constraint. Thus, we are led to nearly opposite conclusions about the nature of constraint: in the first case, selection is the mechanism of constraint; in the second, constraint is something that resists or opposes selec-