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# THE QUARTERLY REVIEW of BIOLOGY



## ARBOREAL CLAMBERING AND THE EVOLUTION OF SELF-CONCEPTION

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### ABSTRACT

*A fundamentally new psychology related to the ability to conceive of limited aspects of the self may have evolved in the ancestor of the great ape/human clade. Existing models of the evolution of primate intelligence do not provide an adequate explanation of the apparent restriction of this phenomenon. We propose that the capacity for self-conception evolved as a psychological mechanism enabling large-bodied, highly arboreal apes to cope with problems posed by the need to negotiate their way through a habitat that was fragile due to their body size. First, we briefly outline the case for believing that a new psychology related to self-conception evolved during the Miocene in the ancestor of the great ape/human clade. Next, we examine the existing models of the evolution of primate intelligence and assess their ability to account for the evolution of self-conception. Finally, we offer details of our alternative model, along with a series of predictions that can be derived from it.*

### THE EVOLUTION OF SELF-CONCEPTION

THE EXISTENCE OF the self-concept poses a difficult problem for a wide range of academic disciplines ranging from evolutionary biology to developmental, comparative and social psychology. In its most sophisticated form, self-conception includes an awareness of the self as (1) an object of knowledge, (2) the subject of experience, (3) an

entity that exists through time, and (4) a causal agent. In adult humans, all of these dimensions (and more) are present and demand explanation from the perspectives of various disciplines. For example, from an evolutionary perspective it remains unclear when various aspects of the self-concept evolved. There is evidence, however, that at least one (and perhaps the most primitive) aspect of self-conception—the ability to conceive of the self

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as a causal agent — evolved quite recently. Indeed, the best available evidence suggests that it is restricted to humans and some of the great apes. In this article, we develop an evolutionary model to explain why humans and great apes appear to be unique in possessing a self-reflective psychology that appeals to itself as the explanation for the consequences of self-generated actions.

#### SELF-PERCEPTION VERSUS SELF-CONCEPTION

Before we examine the evidence for this ability in great apes and human infants, it is important to distinguish self-conception from other related psychological processes and capacities, and in particular, self-perception. Butterworth (1992) has recently summarized the various forms of self-knowledge that an infant human, for example, may possess that are gained through perceptual experience and transferred into memory; he has labeled this type of knowledge *self-perception*. Thus, much information about the self is available strictly through proprioceptive and kinesthetic feedback, without any of it being conceptualized. Such forms of self-perception (and hence self-knowledge) can be sharply contrasted with *self-conception* (the organism's representation of itself as an object or agent that possesses various perceptual and causal abilities). Self-conception presumes that an organism can conceive of itself, whereas self-perception does not.

A diverse array of data suggests that humans formulate a self-concept in the middle of the second year of life (18–24 months). The cluster of abilities that emerge at this age in children suggests the development of a capacity to reflect on their own mental processes (see Gopnik, 1982). At this point, children recognize themselves in mirrors, engage in symbolic play, produce simple acts of altruism, participate in reciprocal cooperative actions with others, comment on the failure of self-generated plans, display mastery smiles upon successful completion of tasks, use mental states referring to desires, spontaneously sort objects using second-order classification rules, appropriately deploy the personal pronouns “I-me-you,” and display the self-conscious emotions (Amsterdam, 1972; Lewis and Brooks-Gunn, 1979; Leslie, 1987; Zahn-

Waxler and Radke-Yarrow, 1982; Brownell and Carriger, 1990; Gopnik, 1982; Kagan, 1981; Bartsch and Wellman, 1995; Langer, 1986; Bates, 1990; Lewis et al., 1989). It is possible that these diverse behaviors are all manifestations of an underlying change in the representational system of infants, a change that allows, among other things, for the representation of the self as a causal agent (see below). Butterworth (1992) has pointed out, however, that developmental psychologists have yet to specify how the neonatal capacity for self-perception gives rise to the young child's development of self-conception. Similarly, comparative psychologists, primatologists, and physical anthropologists have not produced a compelling, testable hypothesis concerning the evolutionary emergence of self-conception.

#### SELF-RECOGNITION IN MIRRORS

Many methods have generated data implicating the period between 18 to 24 months as a time in which self-conception emerges in humans. One of these methodologies, self-recognition in mirrors, has been used extensively with both humans and nonhuman primates. Among primate and nonprimate species tested to date, only orangutans, chimpanzees, a single abnormally reared gorilla, and humans are capable of self-recognition in mirrors. Children typically show signs of self-recognition at around 18–24 months of age (Amsterdam, 1972; Lewis and Brooks-Gunn, 1979). Adolescent and adult chimpanzees and orangutans initially respond to their reflections with a variety of social behaviors, strongly suggesting that they interpret the image as a conspecific. After anywhere from 10 minutes to several days, however, many of these social behaviors are replaced by self-exploratory behaviors in which the animals direct their behavior toward previously unseen parts of the body, such as the eyes, ears, mouth, and ano-genital region (see Figure 1; Gallup, 1970; Lethmate and Dückler, 1973; Suarez and Gallup, 1981; Povinelli et al., 1993). In addition, if the animals are anesthetized and marked with a red dye on their eyebrow ridge and ear, upon recovery they do not make systematic efforts to touch the mark until they have an opportunity to see

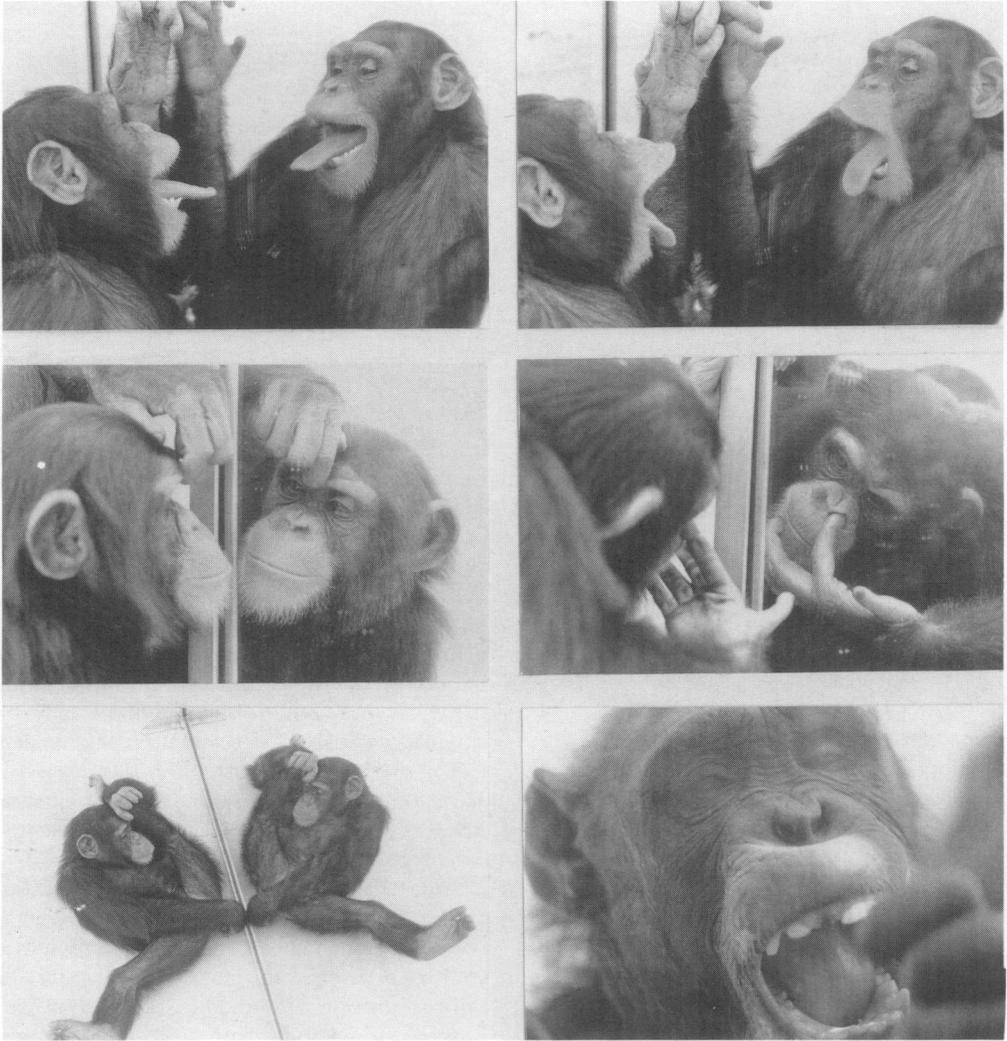


FIG. 1. CHIMPANZEES USING MIRRORS TO ENGAGE IN CONTINGENT FACIAL MOVEMENTS (TOP ROW) AND SELF-EXPLORATORY BEHAVIORS.

themselves in a mirror (Gallup, 1970). These patterns are not characteristic of all chimpanzees and orangutans, but a significant proportion show clear evidence of recognizing themselves in mirrors, and in the case of chimpanzees, developmental trends in this capacity have been identified (see Swartz and Evans, 1991; Lin et al., 1992; Povinelli et al., 1993).

In striking contrast to chimpanzees and orangutans, no other primate or nonprimate

species tested thus far have displayed evidence of self-recognition (reviews by Anderson, 1984; Povinelli, 1987; Gallup, 1991). In two-and-a-half decades of research, no species outside the great ape/human clade have displayed evidence of using mirrors to explore aspects of themselves that they cannot otherwise see (cf. Fig. 1). And none have shown compelling evidence of using mirrors to locate and then touch experimentally-placed marks on their

TABLE 1  
*Primate Species Tested Unsuccessfully  
 for Self-Recognition*

Prosimii	brown lemur ( <i>Lemur fulvus</i> )
	black lemur ( <i>L. macaco</i> )
	ring-tailed lemur ( <i>L. catta</i> )
Anthropoidea	
Platyrrhini	
Callitrichidae	pygmy marmoset ( <i>Cebuella pygmaea</i> )
Cebidae	capuchin ( <i>Cebus appella</i> )
	spider monkey ( <i>Ateles geoffroyi</i> )
	squirrel monkey ( <i>Saimiri sciureus</i> )
Catarrhini	
Cercopithecoidea	
vervet monkey ( <i>Cercopithecus aethiops</i> )	
olive baboon ( <i>Papio cynocephalus anubis</i> )	
hamadryas baboon ( <i>P. c. hamadryas</i> )	
mandrill ( <i>Mandrillus sphinx</i> )	
rhesus monkey ( <i>Macaca mulatta</i> )	
Japanese macaque ( <i>M. fuscata</i> )	
celebes macaque ( <i>M. tonkeana</i> )	
long-tailed macaque ( <i>M. fascicularis</i> )	
stump-tailed macaque ( <i>M. arctoides</i> )	
lion-tailed macaque ( <i>M. silenus</i> )	
pigtailed macaque ( <i>M. nemestrina</i> )	
Colobinae	(none tested)
Hylobatidae	
lar gibbon ( <i>Hylobates lar</i> )	
agile gibbons ( <i>H. agilis</i> )	
Pongidae	
lowland gorilla ( <i>Gorilla gorilla gorilla</i> )	

Sources: Anderson (1983), Anderson and Roeder (1989), Benhar et al. (1975), Bayart and Anderson (1985), Collinge (1989), Eglash and Snowdon (1983), Fornasieri et al. (1991), Gallup (1970), Gallup (1977), Gallup (1982), Gallup et al. (1980), Ledbetter and Basen (1982), Lethmate and Dücker (1973), Suarez and Gallup (1981), Platt and Thompson (1985), Itakura (1987a,b)

faces, although they are quite interested in similar marks placed on bodily regions that can be seen directly. Although we cannot do justice to the large number of studies that have been conducted, Table 1 provides a list of species that have been unsuccessfully tested to date. Many of these studies have employed control procedures and manipulations explicitly designed to rule out methodological problems and to assist monkeys in recognizing themselves (Anderson, 1984; Gallup, 1991),

yet none of these efforts have identified monkeys that respond to their mirror images like chimpanzees and orangutans—despite some assertions to the contrary (see Gallup, 1994, for a critical evaluation of these claims).

Gorillas appear to be a special case among species that apparently fail to recognize themselves. Nearly three dozen gorillas (of various ages and rearing histories) have been tested, and have not shown evidence of self-recognition (Suarez and Gallup, 1981; Ledbetter and Basen, 1982; Lethmate, pers. commun., 1993; Povinelli and Shumaker, unpubl. observations). Both Gallup (1985) and Povinelli (1987) have argued that these data are best interpreted as the secondary loss of this capacity in the gorilla lineage. In sharp contrast to the state of affairs with most gorillas, however, one home-reared and intensively tutored gorilla (Koko) has displayed convincing evidence of recognizing itself in a mirror (Patterson, 1984). Povinelli (1993, 1994) has proposed that certain environmental perturbations involving cognitive stimulation during early ontogenetic development may be capable of causing the reappearance of ancestral neurobiological pathways ultimately responsible for this psychological trait, just as interventions in other developmental systems can produce the appearance of other ancestral morphological traits (e.g., Hampé, 1960; Kollar and Fisher, 1980). Thus, although gorillas were once viewed as an anomaly in the context of the evolution of the capacity for self-recognition (Povinelli, 1987), they can now be understood within the broader context of developmental biology. As we explain later, gorillas represent an important focal point for predictions based on our model of the evolutionary emergence of self-conception.

Parker (1991) has reported evidence of contingent facial movements on the part of some gorillas while viewing themselves in mirrors. However, repetitive and exaggerated movements of the limbs and face may not be good indicators that the animals realize the equivalence between themselves and the image in the mirror (see below). They may only indicate that the animals have learned how to control the image. For example, Eddy, Gallup and Povinelli (in press) have demonstrated that young chimpanzees will display these con-

tigent behaviors toward mirrors without displaying any self-exploratory behaviors and without passing mark tests. More importantly, they can also be misled into displaying the contingent behaviors toward videotapes of other young chimpanzees, presumably because they are trying to control the behavior of those animals in the same way as they controlled the behavior of the ones they saw previously in a mirror. In contrast, older animals, who display clear evidence of self-exploratory behaviors (and many of whom pass mark tests), are not similarly misled, and clearly discriminate between videotapes of others and mirror images of themselves.

Heyes (1994) recently criticized the methodology of self-recognition research in nonhuman primates, and concluded that there is no evidence to date that any nonhuman primate can use a mirror as a source of information about its own body. Heyes questions the interpretation of spontaneously occurring self-exploratory behavior, alleging difficulties in distinguishing between ambient levels of self-grooming and the use of mirrors to orchestrate selective, self-exploratory behavior. With respect to the results of mark tests, she argues that while chimpanzees are recovering from anesthesia they display a general increase in face-touching behavior, irrespective of the presence of a mirror. In order to account for species differences on the mark test, she argues that macaques show less face-touching behavior in general. We find Heyes's objections to be generally without merit. To be sure, there are ample methodological problems associated with conducting proper and controlled tests of self-recognition in human infants and other primates (see Gallup, 1994; Povinelli et al., 1993). However, recent methodological advances control for large portions of the problems she isolates with respect to self-exploratory behavior (Povinelli et al., 1993), and decade-old evidence refutes key aspects of her account of the results of mark tests (Suarez and Gallup, 1986). As a case in point, if the results of mark tests were simply the result of increases in general face-touching behavior following recovery from anesthesia, chimpanzees would not display selective face contacts only to those areas that have been marked, which is their typical pattern of response. A

more detailed critique of Heyes's arguments is provided by Gallup et al. (in press).

Self-recognition in mirrors is important in the present context because within a species it may represent a relatively easy-to-detect marker of a developmental transition from an organism capable of self-perception, to an organism capable of both self-perception and self-conception. Gallup (1975, 1982, 1985) has repeatedly predicted that species capable of self-recognition are self-aware, meaning that they are capable of conceiving of their own existence (self-conception). Gallup's model predicts that species that show evidence of self-recognition should display evidence of an awareness of at least some aspects of their own mental states. That is, Gallup has hypothesized that they are reflectively aware of at least some of their own intentions, desires, beliefs, and personality attributes. There is disagreement about the underlying explanation of self-recognition in mirrors, with opinions ranging from authors who believe that it can be explained without appealing to as sophisticated a self-concept as Gallup has hypothesized, to those who believe that it has nothing whatsoever to do with a self-concept (Hobson, 1993; Mitchell, 1993; Heyes, 1994). Because it is critical to our model, we provide below an abbreviated account of our interpretation of the nature of the self-concept needed for self-recognition in mirrors (for additional details see Povinelli, in press).

#### REPRESENTATIONS VERSUS SCHEMATA

As stated above, self-recognition in mirrors appears to be restricted to members of the great ape/human clade. In order to understand the exact nature of self-conception that is the focus of this article, we must first specify the nature of the self-conception that is needed for an organism to recognize itself in mirrors. To do so, it is necessary to review briefly the ways an organism may represent information about objects in the world, including itself. We will show how transformations in the human infant's general representational abilities have direct consequences for its particular representations of the self that causes self-recognition in mirrors. Although the formal account of transformations in an infant's representational abilities is derived largely from the theo-

retical work of Olson and Campbell (1993), its application to self-representation is our own.

Throughout infancy, humans elaborate the capacity to construct action schemata (singular: schema). Schemata are internal (presumably neural) states that are triggered by stimuli in the external world. These neural programs control motor output, and hence they warrant a description as causal structures. Infants advance from the possession of relatively simple action schemata (reaching, grasping, head-turning) to a later elaboration and complex deployment of such schemata (one hand reaches to open a box, the other reaches inside the box, grasps an object, and pulls it toward the mouth). Gradually, such schemata become highly automatized and can be deployed readily and in rapid succession in the presence of relevant stimuli. Through the process of generalization, these schemata are even triggered in appropriate "novel" contexts. But despite their eventual sophistication, these internal neural structures are not representations (as defined here) of the external world. Olson and Campbell (1993) explain: "Schemata are activated by a present object or event; they are causally connected to that object or event but they do not represent that object or event. Their activity is tied to stimulating conditions; consequently there is no need for the activating condition to be held in mind. It is present, and therefore present to the mind" (p. 15).

Thus, despite the complexity of behaviors that action schemata can support, they are not representations, precisely because such schemata are not held in mind in the absence of the objects of perception that trigger them. The most essential aspect of our argument concerning the development of representation is that human infants are limited to schemata-based knowledge until 18 to 24 months of age (Olson and Campbell, 1993).

In contrast to schemata, mental representations are a means of "maintaining a relation (an intentional connection) with an object or event *in its absence*" (Olson and Campbell, 1993, p. 14, italics in original). (Note that this meaning of representation captures its linguistic origins as the "re-presentation" of an object or event in its absence.) This capacity for representation allows an organism simultaneously to have one schema activated by

direct perception, and another that is held in mind in the absence of direct perception. One important consequence of the capacity for representation is the ability to form a relation between the two schemata. Such relations between schemata are called propositions. Propositions are statements (linguistic or imaginal) that embody relations between separate schemata. Thus, with the advent of representational capacity, many types of propositions become possible. For example, identity or equivalence relations become possible: "This (object of perception) *is a ball* (held in mind)." Similarly, classification becomes possible on the basis of hierarchical categories: "This ball (object of perception) *is a toy* (held in mind)." Other relations become possible as well: "The ball (held in mind) *is in* that box (object of perception)." Also, and critical to our hypothesis, causal attribution should become possible: "This event (object of perception) *was caused by* that action (held in mind)."

#### THE SELF AS A CAUSAL AGENT

Having sketched our view of representational development in humans, we now turn to the question of why self-recognition in mirrors coincides with the emergence of representation-based knowledge and is impossible with only schema-based knowledge (details provided by Povinelli, in press). First, let us consider the organism with only schema-based knowledge. By definition, it has no resources that allow it to perceptually attend to an object or event and simultaneously to relate that thing in propositional form to something else not present. Upon confronting a mirror image of itself, an organism may learn many procedural rules (action schemata) that result in payoffs. For example, it may learn about the contingency between what it sees in a mirror and what is happening in real space behind it (e.g., Itakura, 1987a). As adults, we know that the mirror images are a particular form of representation of events behind us, but in principle one need not know this to learn to respond appropriately by turning around when confronted with interesting events in the mirror. Further, the organism may learn (through proprioceptive/kinesthetic feedback, or self-perception) that when it moves, so too does the image. Indeed, with sufficient expo-

sure, it may even learn to manipulate aspects of the image in the mirror. But note that although a large inventory of such schemata may be constructed and deployed, the image in the mirror (the object of perception) bears no intentional relation to anything else. In particular, for the organism that is observing itself, the image has no relation to the self precisely because the self cannot be re-presented.

Now consider how different a confrontation with a mirror would be for an organism with the ability to represent itself. Although initially the organism would not have complete knowledge of its physical appearance, it would enter the situation already having formed certain representations of itself (these include representations of its actions, desires, and goals). Unlike organisms who possess only schemata, this organism has the capacity to form a relation between its object of perception (the behaving mirror image) and other things not directly available to perception (its knowledge about itself). One particular type of proposition seems likely to be formed very rapidly: "That action by the mirror-image (object of perception) *was caused by* me (held in mind)." Furthermore, with sufficient experience with mirrors, another proposition, expressing an equivalence relation, becomes possible: "That (object of perception) *is about* (or *refers to*) me (held in mind)." We propose that the ultimate psychological cause of an organism's arriving at the conclusion that the image is equivalent to itself is the recognition of the causal relation between its actions and what is occurring in the mirror. Once the organism forms an equivalence relation between what it sees in the mirror and its existing self-representation, it then assumes that what is true of the mirror-image is true of itself and vice versa. This proposition of equivalence motivates what Povinelli et al. (1993) have referred to as self-exploratory behaviors (seeking additional information about the self by use of the identity relation), and explains why, after an organism has incorporated the new visual information about its physical appearance into its internal self-representation, it will reach up to touch marks that it did not previously know were present.

To summarize, self-recognition in mirrors appears to be restricted to members of the

great ape/human clade, and thus appears to have arisen in the common ancestor of the clade sometime after its differentiation from the rest of the hominoid lineage. Mirror self-recognition implicates the presence of a particular form of self-conceptual ability, the ability to ascribe to the self the consequences of the self's actions. The problem of understanding the evolution of the type of self-conceptual abilities that unite the great ape/human clade (with caveats concerning gorillas) thus becomes the problem of determining when and why schemata-based knowledge of the self's actions became insufficient to cope with the ecological circumstances faced by the group's common ancestor. There are currently two general frameworks available for understanding the forces driving the evolution of primate intelligence. We will examine each of them in turn in order to assess their ability to address the evolution of self-conception in the great ape/human lineage.

#### THE SOCIAL INTELLIGENCE HYPOTHESIS

Proponents of the social intelligence hypothesis have argued that group living may have provided the context for the evolution in primates of sophisticated mental abilities for keeping track of social complexity (Jolly, 1966; Humphrey, 1976). One can readily imagine that an understanding of mental states would be advantageous since it would allow an organism to anticipate the moves of competitors, or even to manipulate competitors, perhaps by manipulating their beliefs (de Waal, 1982; Whiten and Byrne, 1988). A possible application of the social intelligence hypothesis in the present context is that an organism that is explicitly aware of its own mental states could also engage in long-range planning, which could clearly be to its benefit.

The problem with the social intelligence hypothesis is that many species of monkeys, prosimians, and nonprimates in general are at least as social as the great apes (and in some cases more so), yet show none of the markers of understanding mental states in themselves or in others, and display no evidence of self-conceptual abilities (Gallup, 1982, 1985; Povinelli, Parks, and Novack, 1991, 1992; Cheney and Seyfarth, 1990). Thus, the social intelligence hypothesis does not appear to provide

an adequate framework for understanding the evolution of a unique psychology related to self-conception in the ancestor of the great ape/human clade. Although it can clearly specify the competitive advantages of being socially intelligent in a social group, and may provide an explanation of why social monkeys could be more intelligent than more solitary species, it cannot explain why the capacity for self-conception is restricted to the great apes and humans.

#### MODELS OF ECOLOGICAL INTELLIGENCE

A second class of models of the evolution of primate intelligence argue that the demands imposed by the need to find food led to the emergence of sophisticated mental capacities. For example, Milton (1981) has proposed that the benefits associated with being able to remember the spatial location and phenological patterns of a diverse assortment of plant foods, including ephemeral patches of ripe fruit, have driven the evolution of primate intelligence. Regardless of the specific merits of the model, it does not explain the psychological differences between the great apes and humans on the one hand, and other primates on the other. What is uniquely challenging to a chimpanzee, for instance, when foraging for fruit, as compared to a gibbon or a long-tailed macaque? It is true that the great apes are larger than all other primates, but they do not spend more of their day foraging than other species with comparable diets. Nor do they appear to be faced with more complex problems related to remembering the spatial distributions of ephemeral resources than, say, baboons (e.g., Boesch and Boesch, 1984; Sigg, 1986).

A second model argues that a specific mode of foraging, what Parker and Gibson (1979) refer to as "extractive foraging," may play a causal role in the development of higher levels of sensorimotor intelligence or brain size in general. While intriguing in its specificity, this model does not account for the fact that other mammals with the same level of sensorimotor intelligence (stage 6), do not employ an extractive foraging strategy (domestic dogs, for example, Gagnon and Doré, 1991). In addition, the extractive foraging model does not adequately explain why some types of extractive foraging (for example, that

shown by chimpanzees, capuchin monkeys and aye-ayes) are expected to drive the evolution of intelligence, but not the extractive foraging of woodpeckers, squirrels, and other mammals. Regardless of the actual merits of the extractive foraging model, the most important point in the present context is that it does not explain the emergence of specific forms of self-conception that may exist in most representatives of the great ape/human clade.

#### A NEW MODEL OF THE EVOLUTION OF SELF-CONCEPTION

We now present our model, which argues that self-conception initially evolved as a psychological mechanism to facilitate planning and execution of unusually flexible locomotor patterns. We propose that these patterns were used by large and highly arboreal ancestors of the great ape/human clade to meet challenges related to habitat structure, in particular, crossing gaps between trees. In short, we hypothesize that the unusual locomotor solutions adopted by these large-bodied apes drove the evolution of self-conception. We argue that the orangutan has deviated least from the ecological context of these ancestors, and thus provides an excellent living model for testing the hypothesis. We set the stage for our model by comparing the locomotion of several primate species and conceptualizing such locomotive behavior in psychological terms. We then outline our model, which explains how a peculiar set of circumstances related to arboreality and body weight might have selected for the evolution of self-conception.

#### BACKGROUND: COMPARATIVE LOCOMOTION OF THREE SYMPATRIC SPECIES

To provide a basis for our hypothesis, we will detail a series of relationships among habitat structure, body weight, and locomotion. In order to illustrate these relationships, we will focus on three species of primates in the rainforest in northern Sumatra, Indonesia.

The long-tailed macaque (*Macaca fascicularis*) resembles a smaller and more gracile version of the better known rhesus macaque. Long-tailed macaques are widely distributed in Southeast Asia. Adults at our study site weigh about 3.5 kg (females) to 5.5 kg (males). They are highly arboreal, and at least 90 per-

cent of their activities take place in the canopy. When locomoting during traveling and feeding, macaques spend a clear majority of their time walking or running quadrupedally along or across various substrates, typically lianas (woody vines) and horizontal or slightly inclined tree branches (Cant, 1988). They typically move in a pronograde fashion, with their body parallel to the surface on which they are traveling and their ventral surface downward, somewhat in the manner of squirrels in trees or dogs on the ground. The limbs of macaques tend to swing through restricted planes parallel to the body's median plane (a plane passing through vertebral column and sternum). Nearly all of macaque locomotion takes place above the support, in a horizontal, diagonal or vertical direction. When crossing gaps between trees, long-tailed macaques use leaping in about 40 percent of crossings, and "walk-through" along and between adjacent branches and/or lianas in the rest (Cant, 1988).

The second species is the siamang (*Hylobates syndactylus*), which along with gibbons is a member of the family Hylobatidae (lesser apes). Siamangs inhabit parts of peninsular Malaysia and Sumatra, and weigh about 11 kg. They are entirely arboreal, feeding and traveling exclusively in the canopy. In sharp contrast to macaques, their body orientation is usually orthograde (upright). Almost half of siamang locomotion is brachiation, in which the animal swings along under branches, suspended by its forelimbs (Fleagle, 1976). Most of the rest of their locomotion is defined as "climbing" by Fleagle (1976).

Finally, the orangutan (*Pongo pygmaeus*), is one of the great apes, along with chimpanzees and gorillas. Orangutans are now found only on the islands of Borneo and Sumatra, although they were more widespread on the Southeast Asian mainland during the Pleistocene. Adult females weigh approximately 40 kg and adult males weigh 80 kg or more. In Sumatra, orangutans are almost entirely arboreal, although adult males occasionally come to the ground to chase each other. In Borneo, females normally remain in the canopy, while males travel on the ground and ascend trees to feed.

Orangutan locomotion can be both com-

pared to and contrasted with that of macaques. Both engage in climbing and walking quadrupedally along supports. But macaques employ at least two styles of locomotion that orangutans typically do not: leaping and dropping. More important, however, is the fact that orangutans locomote in ways that macaques never do — brachiation, tree-swaying, and especially clambering. In clear contrast to macaques, they display a predominantly orthograde body orientation, exceptionally long upper limbs, and great mobility at the shoulder. Orangutans also possess uniquely great mobility at the hip. From 10 to 20 percent of their locomotion is brachiation, and the rest is mostly clambering, a form of locomotion in which the body is orthograde, with various combinations of the four appendages grasping supports in different directions, both above and below the animal. Clambering typically includes suspension of considerable body weight by the forelimbs and hindlimbs (Cant, 1987; Sugardjito and van Hooff, 1986). Cant (1987) has reported that adult female orangutans spend over 50 percent of their travel time using this complex form of locomotion.

#### FOREST CANOPY STRUCTURE AND BODY WEIGHT: LOCOMOTOR PROBLEMS

There are a number of important features of forest structure to be noted when considering the locomotor styles of the three species described above. One key aspect is vertical tree trunks, which are relatively stable but often separated horizontally from one another by substantial distances. The branches of trees stretch outward from the trunks, and in some cases they extend toward neighboring trees. Branches taper toward their ends, however, and as they become thinner they also become weaker, less stable, and deform downward more readily under the animal's weight (tending to topple the animal off the branch). It should be noted that even narrow gaps between trees are typically between the ends of thin branches. Furthermore, most fruits and leaves are attached to the thin ends of branches.

A second important feature of rainforest structure is lianas, which typically extend upward from the ground to the main canopy, although some provide more or less horizontal

links between tree crowns. Experimental research has demonstrated that the stability and strength of lianas are highly variable (Cant et al., 1990).

From the perspective of an animal inhabitant, forest structure presents several distinct problems that must be solved for successful life in the canopy. For example, an animal must possess locomotor skills for climbing large tree trunks, acquiring fruit and leaves located on thin supports, and crossing gaps between trees.

All other aspects of an animal's existence and reproduction (fitness) depend directly upon the quality of its solutions to these locomotor problems (see Cant, 1992a). Yet the severity of most habitat problems is not the same for all animals; body weight is a critical factor, for increasing body weight produces at least three crucial changes in the properties of a support that is used for locomotor or postural activities. One change, almost by definition, is an on-average reduction in the strength of the habitat relative to the animal. The additional forces placed on branches and lianas by a heavier body reduce the relative strength of each support. Note that for an animal with the body size of a long-tailed macaque, nearly all supports provide a significant safety factor. This is not the case for an orangutan, who, because of its larger mass, will find a significantly reduced safety factor in any given support. The other two changes in the properties of supports with increasing body weight is that they become less stable and tend to deform downward. These changes result in a greater likelihood of falling for larger bodied animals, and, in some cases, an increase in the width of gaps in the canopy due to downward deformation, at least in situations where branches are positioned horizontally.

A final point is that larger animals are more fragile (relative to body weight) than smaller ones, and thus are at greater risk of serious injury or death if they fall out of the canopy. For instance, a long-tailed macaque might be able to walk away from a 10-meter fall from the canopy, whereas a similar fall would likely prove fatal for an adult male orangutan.

In reflecting upon the problems identified above, we conclude that crossing gaps be-

tween trees is the single most important problem of habitat structure for arboreal animals of moderate (10 kg) to large weight (40 kg and greater). Furthermore, we suspect (for reasons explained below) that the gap-crossing problem becomes increasingly severe for animals that weigh more than 10 kg.

#### SOLUTIONS TO LOCOMOTOR PROBLEMS

From the preceding discussion it is evident that both habitat structure and body weight are factors in problems to which locomotor and postural behavior may provide solutions. But how do primates with different body weights actually solve these problems? Data on the locomotor behavior of long-tailed macaques, siamangs, and orangutans (as well other species) have typically been presented as differences in frequency of use of specific locomotor patterns (Fleagle 1976; Sugardjito and van Hooff, 1986; Cant, 1987, 1988). This approach is useful for many purposes, including understanding the evolution of the primate postcranial skeleton. However, to date this approach has not emphasized important qualitative differences in how orangutans and other arboreal species solve the locomotor problems described above. Below we examine some of the solutions adopted by orangutans, siamangs, and long-tailed macaques in the context of exploring the interrelationships of body size and habitat structure.

*Suspension.* A fundamental aspect of locomotor solutions is whether the animal is limited to moving above supports, or whether it also suspends below them. As already described, long-tailed macaques are entirely above-support in their locomotion, whereas siamangs and orangutans exhibit a considerable amount of suspensory locomotion below supports. Suspensory modes should be especially useful when dealing with unstable supports, because a suspending animal has in effect already fallen off the support (but remains attached), and its body mass tends to reduce oscillations of the branch or liana (Grand, 1972). Bearing in mind that increased body weight implies decreased branch stability, one may predict that heavier animals should suspend more often than smaller ones (Napier, 1967; Cartmill, 1985).

*Multiple supports.* Another aspect of locomo-

tor behavior and habitat structure is the number of supports that an animal uses simultaneously. Whereas a small animal is normally safe when using a single branch, a heavier one experiences increased risk of the branch breaking. Thus heavier animals are expected to use multiple supports more often than smaller animals, and should be more able to do so because greater weight is accompanied by greater reach of the limbs. Consistent with this prediction, about 70 percent of long-tailed macaque movement is along single supports, whereas almost 70 percent of orangutan locomotion is across multiple supports (Cant, 1988, 1987). Quantitative data are not available for siamangs, but we predict they are intermediate with respect to use of supports.

*Habitat compliance.* Compliance (deformation) under an animal's weight is usually thought of as contributing to instability and the danger of falling. But there are three different behavioral responses to compliance, and they exhibit strikingly different cost/benefit relationships: adjusting to compliance (for example, an animal at the end of a leap waits until branch oscillations cease before it moves onward), ignoring compliance (often by suspensory locomotion), and using compliance to help propel itself through the canopy. Our recent work in northern Sumatra has revealed that long-tailed macaques usually must adjust to compliance and seldom use it, siamangs frequently ignore it, and orangutans very often use compliance. Orangutans exhibit a variety of methods of utilization, including tree-swaying, in which the individual enters a small to moderate size tree with a flexible trunk, and shifts its weight to the side facing the direction of desired progression. As a consequence the tree sways in that direction, and the animal then disembarks into another tree or liana that could not have been reached directly without using the compliance of the swayed tree. Another form of utilization is to swing on a downwardly inclined branch, using it like a trapeze, again to transport laterally through space (Cant, 1992b). The suspensory locomotor patterns of orangutans facilitate use of habitat compliance because orthograde suspension is based on great mobility of limbs, and that mobility provides flexibility in dealing with diversely oriented supports of vari-

able compliance. Other researchers have elaborated on some of these aspects of orangutan locomotion in the context of understanding their capacity for tool use and general intelligence (see Chevalier-Skolnikof et al., 1982).

Although the above problem-solution complexes may appear to be relevant only to large-bodied animals, this is not the case. Even fairly small arboreal primates like long-tailed macaques face problems of habitat instability, fragility, and gaps. A key difference, however, is that they are able to solve these problems with relatively discrete behaviors, moving mostly along single supports, without having frequently to assimilate and respond to new information about their physical surroundings. Animals of this size usually adjust to or ignore habitat compliance; the severity of the problems they face does not often require use of compliance, and their modest weight does not facilitate it. This does not mean that all animals of about 5 kg locomote like macaques. Gibbons are only slightly larger and yet exhibit a great deal of suspensory movement (brachiation), much of which is across multiple supports. The important point is that a 5 kg animal can behave in the manner of a long-tailed macaque, and in fact gibbons, although their gross behavioral patterns differ markedly, appear quite "stereotyped" (term discussed below). With increasing body size the major changes we expect to see, illustrated in 11 kg siamangs, are an increase in the use of multiple supports, and the use of mechanically more diverse arrangements of supports, which the animal must respond to by assimilation of information and behavioral accommodation. As body weight increases beyond that of a siamang, we would expect to see further decreases in the use of stereotyped locomotor patterns and increasing use of habitat compliance, but it is unclear at what weight the severity of locomotor problems approaches that faced by orangutans. There are very few primates between 11 and 40 kg that habitually travel through the canopy, rather than traveling on the ground and climbing trees to feed, which is the typical pattern for chimpanzees.

#### NONSTEREOTYPED LOCOMOTION

As an initial characterization, we propose that the problem-solution complexes we have identified lead to gross differences in locomo-

tor styles among arboreal organisms of different body weights. These differences can be summarized as stereotyped or nonstereotyped locomotion. Borrowing the terminology of developmental psychology, and considering the qualitative aspect of solutions to locomotor problems, we argue for the need to reconceptualize the *modes of behavior* typically identified in locomotor studies as distinct *action schemata*. An action schema can be defined as a discrete learned action sequence that the organism has incorporated into its behavioral repertoire. Rather than focusing exclusively on the percentage of time an animal spends executing a given locomotor schema, we can attempt to quantify the diversity of discrete action schemata of locomotion used by a given species.

Macaques show a number of discrete action schemata, including quadrupedalism at different speeds and angles, short lunges across gaps (sometimes accompanied by reaching across the gap and pulling a branch or liana toward them), leaping, dropping, and shinnying down vertical tree trunks. In contrast, orangutans appear to possess far fewer discrete action schemata, to a large degree because of the lack of leaping, dropping and lunging across gaps. As indicated earlier, orangutans spend the majority of their time clambering. Upon careful reflection, clambering includes a seemingly infinite number of action schemata in which the animal's locomotion is continuously modified during gap crossings in the canopy. Thus, for instance, an animal may reach out and pull in a group of terminal branches with one appendage, simultaneously use a different limb to grasp a liana, pause and survey its surroundings, use a third limb to seize another group of thin branches or lianas, and finally release its last hold on the original support and swing across the gap. During such bouts of locomotion it is important to note that first, the animal's limbs may be related to each other in a variety of angles owing to their tremendous rotational ability at the hip and shoulder joints, and second, that the animal's trunk may be oriented in a variety of ways relative to the direction of movement. These observations are relevant because they make the point that the behavioral modes traditionally referred to as clambering bear a conceptual, but not necessarily kinematic, resemblance to one another.

Our observations of 40 kg female orangutans, which are at most one-half the weight of males, have led us to conclude that the locomotor problems confronted and solved by orangutans are much more severe than those dealt with by macaques and siamangs, and their solutions are radically different, particularly for crossing gaps. Habitat compliance, which is weight-dependent, is of major importance for orangutans, as the structure of an individual's habitat changes in response to its presence, and changes further in response to its movements. Orangutans must thus solve the problem of maneuvering through a highly deformable habitat in which the immediate structural elements available for use change in position relative to one another and to the animal as it moves. Compliance and its necessary effect of changing structural context occur throughout an orangutan's arboreal habitat, both between and within trees. It is more important during gap crossings, however, because the choices available to an animal lacking the ability to leap are limited by the distribution and proximity of branches of neighboring trees, and by the location of lianas. In contrast, within a tree the animal has the option of following major branches, although the resulting pathway might be longer than if it pursued a more direct path across branches of more variable size and compliance.

In addition to the magnitude of compliance, we call attention to its regularity. It is our impression that with increasing body weight of the animal deforming habitat elements, compliance is less regular in direction, perhaps because more linked branches or lianas of different orientations are involved in any deformation event. In observing orangutan locomotion, it often appears that the animal attempts one method of dealing with a problem, and if something goes wrong, it then changes its behavior. In many cases what goes wrong is that the habitat does not comply as the animal's initial actions led one to believe it had predicted. A comparable pattern is not apparent in the much more fluid and seemingly less corrected travels of macaques and siamangs.

We thus argue for a distinction between locomotor systems governed exclusively by

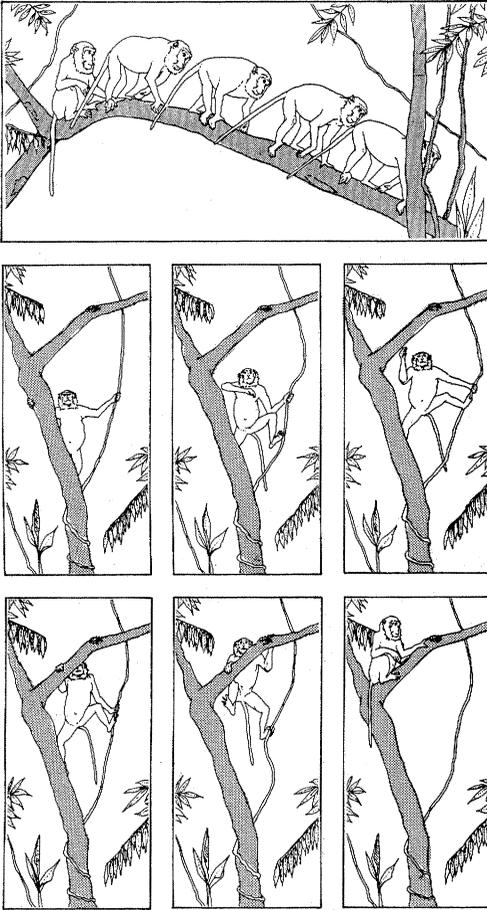


FIG. 2a. TYPICAL LOCOMOTOR SCHEMATA OF A 5.5 KG LONG-TAILED MACAQUE.

highly stereotyped action schemata, and those that exhibit a tremendous degree of flexibility, both during their use and between each successive use. The distinction is an important one, as is immediately apparent from a comparison of Figures 2a-c, which show samples of typical locomotor schemata of long-tailed macaques, siamangs, and orangutans in northern Sumatra. The differences can best be described by noting that although macaques, for instance, have several arguably distinct action schemata that they employ with reasonable frequency, many of them strongly resemble one another in their overall design. It seems clear that, in

the case of macaques, vertical, horizontal, and diagonal quadrupedalism, lunging, leaping, and even dropping, all revolve around the morphological constraints of a quadrupedal gait. In addition, each schema can be executed with a high degree of automaticity and requires little modification until its completion, followed by transition to the next schema. Although we have made less intensive observations of siamangs than of macaques and orangutans, it appears that this species is intermediate in terms of stereotypy (see Fig. 2b).

In summary, macaque locomotion appears relatively stereotyped, exhibiting the predominant use of discrete action schemata with a degree of repetition, with little assimilation of new structural information and accommodation to diverse structural contexts. Orangutan locomotion appears relatively nonstereotyped, consisting mostly of nondiscrete and highly variable schemata in which limb maneuvers are not repeated very often, and there is a great deal of assimilation of changing structural contexts and accommodation to them (see Fig. 2c). This is not to say that species other than orangutans are unable to acquire new action schemata, but rather that in the case of orangutans several schemata are able to be represented and executed more or less simultaneously in order to produce creative, on-the-spot solutions to immediate problems.

This reconceptualization of locomotion emphasizes that there is a continuous spectrum from the stereotyped to the nonstereotyped. Several aspects of behavior combine to determine the degree of stereotypy, and need to be examined when we look at the stream of locomotor behavior exhibited by an animal as it moves through its habitat. First, it is possible to ask what proportion of locomotion consists of *discrete, readily definable action schemata*. The second component of stereotypy is its *repetitiveness*. A macaque moving along a series of branches of different sizes and orientations essentially uses the same limb maneuvers over and over, whereas orangutans show very little repetition of limb maneuvers. The final component is the nature of the *animal's response to the structural context of its locomotion*. This last factor is especially important to our argument. If our view is correct, then proprio-



FIG. 2b. TYPICAL LOCOMOTOR SCHEMATA OF AN 11 KG SIAMANG.

ceptive feedback is exclusively responsible in macaques for the deployment of alternative action schemata. The animal's proprioceptive system responds to the nature of the supports on which it moves, and adjusts its behavior to their arrangement in space. This appears to be a fairly simple process because its choice of pathway—largely along or across continuous supports—keeps it moving with its eyes and forelimbs facing in the direction of upcoming hand- and footholds, almost all of which will be similar to previous ones. In contrast, the immediate structural context for an orangutan varies greatly from one moment to the

next, and appears to require frequent evaluation and assimilation of new information, as forelimbs and hindlimbs move in diverse directions to accommodate diverse contexts. Also much more variable in orangutans is the positioning of the body relative to its supports—sometimes above, often below, and sometimes a combination of the two (as when the animal uses multiple supports spread out vertically). The orthograde suspension of orangutans contributes to a further reduction in stereotypy because the animal can rotate its trunk around a fixed hand-hold, and thus

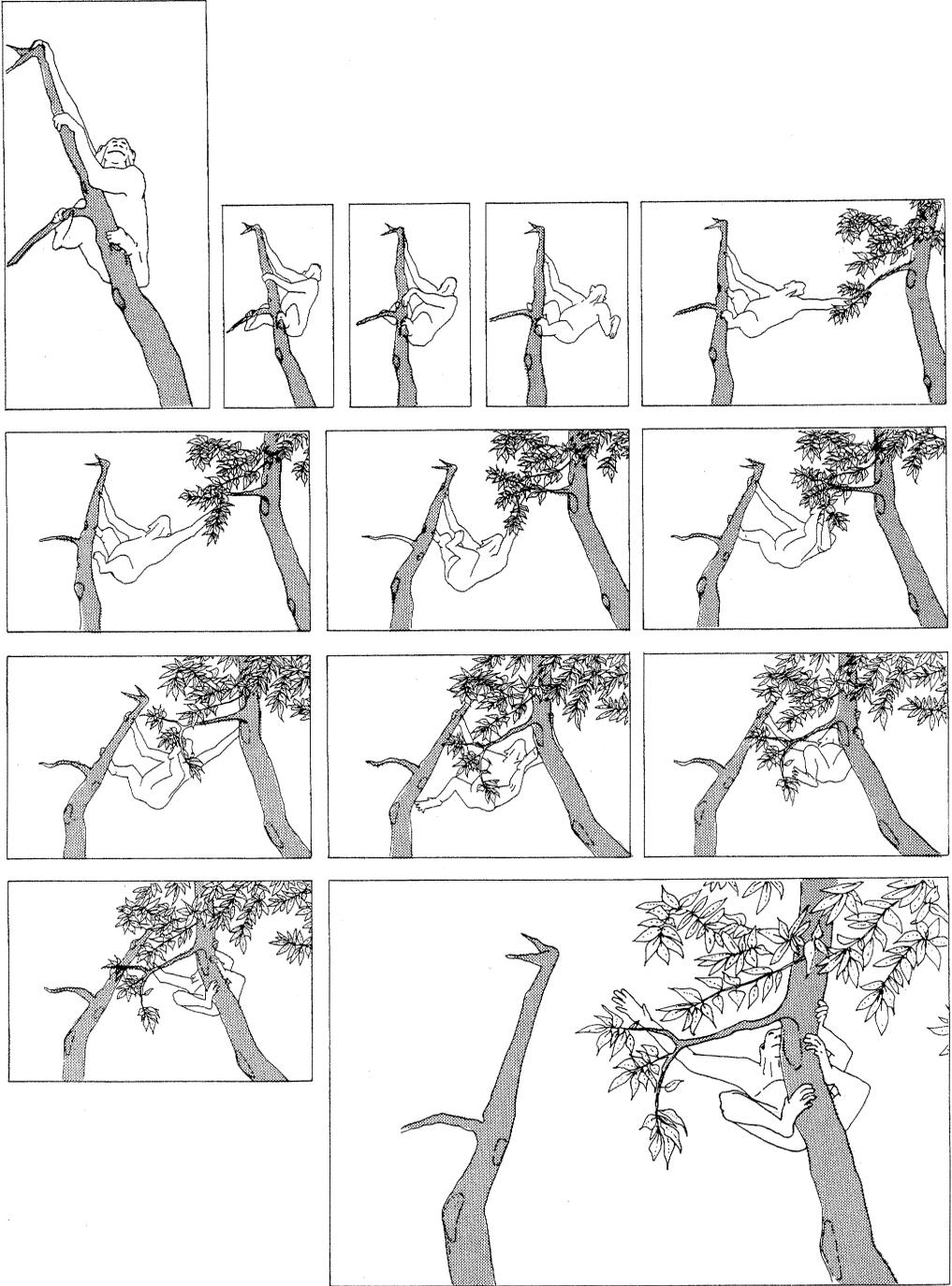


FIG. 2c. TYPICAL LOCOMOTOR SCHEMATA OF AN 85 KG MALE ORANGUTAN.

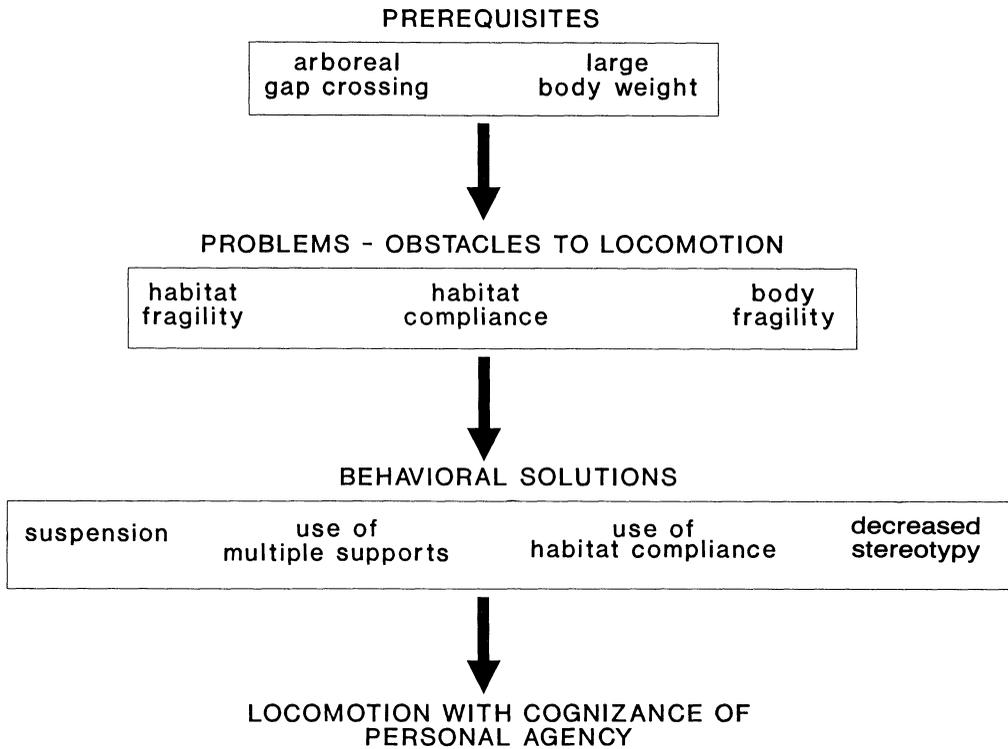


FIG. 3. CONCEPTUAL STRUCTURE OF THE CLAMBERING MODEL OF THE ORIGINS OF SELF-CONCEPTION.

orient its body more variably, and change direction more readily.

#### AN AWARENESS OF PERSONAL AGENCY

We now consider the psychological evolution that may have coincided with the behavioral evolution of this type of body-weight induced clambering. In Figure 3 we depict our hypothesis of the evolution of self-conception by showing classes of phenomena and general relationships, whereas in the text we have previously attempted to indicate specific causal relationships. We hypothesize that each of the problem-solution relationships previously identified contributes to the failure of stereotyped locomotor schemata. In other words, we contend that the evolutionarily primitive psychological mechanisms that regulate routinized action schemata (what Piaget referred to as the sensorimotor system) were no longer sufficient when this combination of problems arose sometime during the Miocene.

We speculate that at some (admittedly unspecified) size beyond that of modern siamangs, an evolutionary increase in body weight led to the disruption of the sensorimotor system's ability to effectively regulate locomotion, for the reasons given above. The large-bodied ancestors of the great apes and humans who crossed gaps in the canopy could no longer employ stereotyped locomotion schemata on such a diverse array of structures, because of deformation and failure of the structures under their weight, as well as their increased difficulty of predicting structural compliance. Rapid transitions between schemata became impossible because the animals were forced to move more slowly in order to avoid the problems outlined above. And finally, the cost of trial-and-error learning became too severe because of the ratio of strength to weight problem described above. The failure of sensorimotor regulation drove the evo-

lution of new behavioral strategies of locomotion, and, we suspect, a new psychological system to augment the more-or-less automatic and unconscious sensorimotor system.

Our hypothesis is that clambering in large-bodied apes who negotiate a habitat that is fragile, unstable, noncontinuous, and unpredictable as a consequence of their body weight, is underpinned by cognizance of one's actions — an ability to engage in a type of mental experimentation or simulation in which one is able to plan actions and predict their likely consequences before acting. We suggest that this is comparable to what Ferguson and Gopnik (1988) describe as the ability of 18-month-old human children “to ‘run through’ possible courses of action and consequences in their heads without having to experience those actions or consequences” (p. 232).

It might be thought that an alternative to evolving a new psychology would be to simply locomote more slowly, and hence become more “cautious.” Although this is true, and indeed is part of our argument, it is by no means the entire picture. A re-examination of Figure 2(c) clearly reveals the special nature of clambering as practiced by orangutans. Clambering is definitely not a simple slowing of some subset of discrete locomotion schemata. We therefore argue that the initiation of “clambering” is not analogous — either kinematically or psychologically — to the initiation of an action schema such as brachiation or quadrupedal running, in which discrete, highly repetitive (stereotyped) patterns of limb and body movements necessarily follow one another.

A central distinction for our hypothesis is the difference between biological systems governed strictly by sensorimotor regulations, and those that possess an awareness of themselves as a causal agent. Although we are by no means committed to his explanations, Piaget (1976) has provided one of the most coherent accounts of the ontogeny and function of the capacity for self-conception (what he alternately labels “consciousness” and “cognizance of one's actions”) in young children. With respect to self-consciousness and action, Piaget noted that “cognizance (or the act of becoming conscious) of an action scheme transforms it into a concept” (p. 332). He

argued that an individual's consciousness of how they solve specific problems is best viewed as the subjects moving from an automatic (and unconscious) sensorimotor regulation of behavior to an awareness of how their own actions cause environmental effects. Although many of Piaget's specific proposals have been challenged in light of recent evidence of the emergence of various kinds of knowledge in infancy, he was well aware of an infant's early implicit knowledge of its own actions. Indeed, his basic distinction here seems strikingly reminiscent of Butterworth's (1992) plea for a conceptual distinction between self-perception (implicit self-knowledge) and self-conception. This distinction between implicit (tacit, procedural) and explicit (conscious, declarative) access to knowledge is widely recognized in the literature on human cognition, and is especially useful in understanding certain neuropsychological conditions such as amnesia and blindsight, in which patients retain many forms of implicit knowledge without attendant conscious access to this knowledge (see Schacter et al., 1988).

In an attempt to explain why this form of consciousness is present at all in humans, Piaget (1976) focused on the proximate level of explanation and noted that “cognizance would . . . appear to be a direct consequence of a failure [of the sensorimotor system] to adapt” to a novel situation (p. 333). He further concluded that “cognizance is always triggered by the fact that automatic regulations . . . are no longer sufficient” (p. 333). “New means,” he wrote, “must therefore be sought out through a more active adjustment; this constitutes the source of thought-out choices, which presupposes consciousness” (p. 333). He was not concerned with the evolution of this capacity, but he was interested in its developmental course in the child, and apparently believed that during early sensorimotor stages children are largely unconscious of their own actions. This notion of the function of conscious access to behavior (and thought) is echoed by other researchers, such as Johnson (1987) who writes, “Conscious access is a higher-order projection of information already available at lower levels of processing. At an unconscious level, action systems and perceptual systems must mutually inform one another of their

ongoing status: Incoming information must be coordinated with outgoing intentions. At a conscious level, access enables the organism to recognize its own states and hence more flexibly direct behavior . . . [and] to plan how one might act" (p. 53). This view of the function of early forms of self-conception is obviously very consistent with our idea that a self-representational system evolved as a means to engage in mental experimentation of one's actions prior to their deployment, in order to more effectively solve logistical problems caused by aspects of the self's behavior.

Thus, if for most organisms sensorimotor intelligence is an adequate psychological system for negotiating the environment and finding food (and storing representations of those actions and locations in memory), then we should not expect to find a widespread distribution of psychologies in which organisms are aware of themselves as causative agents. In contrast, if the proper raw brain material is available, and the organism's commitment to arboreality and large body size is fixed, understanding oneself as an animate object with causative powers would be of tremendous selective advantage. We speculate that this understanding allows an animal to "see" itself in a three-dimensional skein of highly variable fragility, compliance and space, whose properties change in response to its own movements. As it moves with the moving elements of its habitat, being able to visualize itself enhances prediction (mental experimentation or simulation) about the effects of its actions, and facilitates further decision-making when the habitat does not respond as predicted. The ability to attribute to *itself* the cause of a structural problem associated with locomotion would clearly be of great advantage for an arboreal, large-bodied ape in its attempts to solve such problems.

Finally, we suggest that our model could provide an evolutionary framework within which we can begin to understand the emergence of cognitive mechanisms that have been proposed by Frith and Done (1989) and Baron-Cohen et al. (in press) called the Intention Monitor and the Intention Editor, respectively. According to Frith and Done, the Intention Monitor has three functions. First, it

determines if actions that are driven by a goal or plan (a willed intention) resulted in the desired outcome. Second, it monitors the environment to determine if actions that are elicited by external triggers achieve the appropriate outcome. But the key function of the Intention Monitor is that it identifies the source of particular intentions and thus is able to discriminate between actions and effects that resulted from external versus internal causes. Baron-Cohen et al. (in press) argue for a related (but dissociable) mechanism referred to as the Intention Editor. Its function is to edit competing instructions (intentions) whenever there are several intentions activated in parallel. Evidence for the existence and separability of these mechanisms is provided in neurological syndromes such as types I and II schizophrenia and Tourette's syndrome (Frith, 1987; Baron-Cohen et al., 1994). Although it is premature to specify the exact connections between our model and these hypothesized mechanisms, such neural systems are the kinds of structures that would support the mental processing we believe was selected for in the context of the evolution of clambering in large-bodied hominoids in the Miocene. Thus, viewed as a conceptual unit, these mechanisms provide a detailed description of the cognitive structures for which we are providing an evolutionary explanation. If we are correct, such structures should be absent in lineages that differentiated prior to the evolution of the great ape/human clade.

#### TOWARD A SELF-CONCEPT

Although the above model accounts for the evolution of an awareness of the self as a causal agent, it may be less obvious how this relates to an elaborated self-concept—that is, an organism's understanding of itself as an individual entity with its own unique set of desires, beliefs and personality attributes (see Wellman, 1990, for one view of the development of this form of personhood in human children). First of all, a sense of personal agency is not possible without a sense of self-identity. In other words, an awareness of personal agency presupposes an identity onto which that agency can be mapped. In this sense, if one were to evolve a sense of personal agency, one would need to first evolve an explicit set of

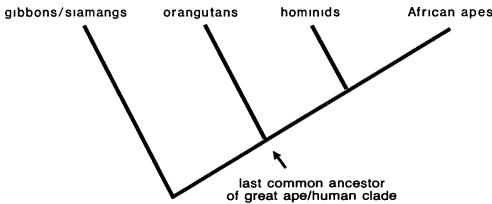


FIG. 4. PHYLOGENY OF THE GREAT APE/HUMAN CLADE, WITH HYLOBATIDS AS OUTGROUP.

core self-attributes. The self is conceptualized as an object that possesses various characteristics, some of which may be psychological. It also seems clear that the very first aspect of the self to be conceptualized would be the definition of the self as agent. Once this sense of personal identity and agency emerges, an understanding of that object (the self) can be elaborated and expanded upon almost indefinitely. All of the many dimensions of the self, including personality traits, intentions, desires, hopes, and knowledge, become at least theoretically possible (see Allport, 1943 for a discussion of the various dimensions of the self). This is not to say that all organisms with a sense of personal agency proceed through an infinite redefinition and elaboration of the self. Indeed, the exact nature of the orangutan's self-concept is not specified; our model predicts that it extends to include agency and desire. Nonetheless, this process of discovery becomes possible, or is allowed for, with the advent of self-conception.

#### THE PHYLOGENETIC CONTEXT OF THE MODEL

The basic relationships of the living large hominoids are shown in the cladogram of Figure 4. There is reasonable consensus about the general shape of the cladogram, with the orangutan lineage diverging before some sort of separation of the African apes and hominids. We do not indicate any precise relationship between the African apes and humans for two reasons. First, there is considerable disagreement as to whether gorillas diverged first, so that humans and chimpanzees are more closely related, or whether the hominids diverged first, leaving chimpanzees and goril-

las to branch later (Marks, 1991, 1994; Rogers, 1993). The second, more important reason, is that the details of the African ape/hominid divergences are not critical to our argument. The dates of the nodes are subject to varying estimates owing to uncertainty about hominoid fossils, which we discuss below.

From a phylogenetic perspective, our model depends on the plausibility that the last common ancestor of the large hominoid clade exhibited locomotor behaviors similar to some orangutan patterns, particularly those that we have proposed to have been crucial in the evolution of self-conception. Because the behavior of Miocene animals cannot be observed directly, we must infer the positional capabilities of the ancestor of the clade from its reconstructed morphology. This is not simple: Despite the large number of fossils from Miocene strata in Eurasia and Africa that have been classified as hominoids, there is no general agreement as to which (if any) were (a) the common ancestor of the great ape/human clade, (b) on the direct line leading to this common ancestor, or (c) on the line between the last common ancestor and the splitting of the African apes and hominids.

Any attempt to reconstruct the ancestral morphotype of the large hominoids is complicated by the small number of extant large hominoids and the morphological diversity they exhibit. As Harrison (1991) has explained, ". . . the living great apes are individually too specialized in their modes of locomotion, and too autapomorphic in their postcranial morphology, to serve as plausible ancestral morphotypes of the large hominoid clade" (p. 236). Nonetheless, Harrison found it possible to infer some basic structural/functional complexes of the ancestral morphotype (as compared to quadrupedal animals) that bear on locomotor capacities for orangutan-style clambering: orthograde orientation of the body; increased potential for raising the forelimbs above the head and for axial rotation at the shoulder, elbow, and wrist; increased abduction and adduction at the wrist; greater rotation at the hip and knee, and inversion and eversion at the ankle (Harrison, 1991). The only Miocene hominoid whose postcranium is adequately known and which possesses the

morphology suitable for these capacities is the late Miocene *Oreopithecus bambolii* from northern Italy, which is estimated to have weighed from 15 or 20 to 40 kg. It is impossible to know where *Oreopithecus* fits phylogenetically, as its cranium (especially its dentition) is very derived, despite its generalized hominoid postcranium (Harrison, 1991).

The principal lesson from *Oreopithecus* is that at some point in the Miocene there was at least one reasonably large-bodied hominoid whose postcranial morphology would have permitted orthograde, forelimb suspension, flexible orientation of the body about fixed handholds, and considerable mobility of the hindlimbs to grasp supports oriented in irregular ways relative to the body. These are the basic components of the locomotor patterns that we suggest were essential in the evolution of self-conception. (It is possible, but much less certain, that the Miocene *Dryopithecus bran- coi* from Hungary had a similar postcranium [Begun, 1992]).

A large hominoid last common ancestor of the great ape/human clade resembling *Oreopithecus* forms a reasonable basis for diversification: Chimpanzees and especially gorillas developed specializations for terrestrial quadrupedalism, whereas orangutans became more specialized to deal with problems of increased body weight while maintaining arboreal suspensory patterns.

Some primate paleontologists might have two reasons to question our use of orangutans as a model. First, the animal may appear to be too specialized to serve as a general model. In response, we believe that none of the locomotor patterns we have observed in orangutans (and have identified as critical to our hypothesis) would have been difficult for an animal like *Oreopithecus*, although some postural behaviors, including hand-foot hang (Cant, 1987) might have been unlikely. In addition, in order for a selection gradient for self-conceptual capacities to have been established in response to the problems associated with increasing body weight, one must posit that the ancestor of the clade possessed generalized locomotor patterns. Orangutan morphology may merely be a somewhat more specialized solution to this problem. Second, some have suggested that orangutans and the

Miocene *Sivapithecus* are sister taxa (e.g., Andrews and Cronin, 1982). If true, this would complicate any reconstruction of the common ancestor of the large hominoids, as *Sivapithecus* combined an elbow like that of modern hominoids with a humeral shaft and wrist implying above-branch quadrupedalism (Rose, 1993). For the present it appears safest to reserve judgment about the relationship of orangutans and *Sivapithecus* (Pilbeam et al., 1990). Orangutan locomotor behavior is thus suitable as a living model for the evolution of self-conception, bearing in mind that no model used in this way should be expected to resemble past forms *precisely*. In addition, *Oreopithecus* is a suitable fossil model of the kind of postcranial morphology that probably permitted the behaviors we view as critical for our hypothesis, without the complicating factor of the exceptionally great body weight of adult male orangutans.

Two extinct primates outside the Hominoidea deserve mention because they were quite large and suspensory. The first, *Palaeopropithecus*, is a Malagasy lemur, weighing perhaps 40 kg, that has been inferred to have locomoted by quadrupedal suspension in the manner of sloths (Godfrey, 1988). We think it doubtful that such a locomotor style would have involved the kinds of nonstereotyped locomotion that our model describes, and thus self-conceptual abilities are unlikely to have evolved. The second extinct primate of interest is *Protopithecus*, from Brazil, probably closely related to *Brachyteles* (the woolly spider monkey), which probably weighed somewhat over 20 kg. Its postcranial morphology suggests orthograde suspensory behavior, perhaps similar to *Brachyteles* (Hartwig, 1995). The combination of large body size and suspensory behaviors, which were almost certainly quite different from *Palaeopropithecus* and may have been similar to extant hominoid suspensory behaviors, suggests that *Protopithecus* might have been under the same sorts of selection pressures as we hypothesize for the common ancestor of the great apes and humans. In general, however, our model is not affected by whether or not there were (or are) other species capable of self-conception. For example, if *Protopithecus* did evolve the relevant conceptual abilities, this convergence

would support the model. On the other hand, the absence of these abilities could simply indicate either that their locomotor patterns were different, or that there was something unique about the neural machinery of the great ape/human ancestor (but not these other primates) that allowed for the selection of self-conception.

#### PREDICTIONS OF THE MODEL

The model we have offered above provides an explanation of the ultimate (vs. proximate) cause of the capacity for self-conception in the great ape/human clade. As currently formulated, it represents a broad, causal argument of the adaptive significance of a sense of personal agency in the context of locomotion in large-bodied apes. As such, the model can be used to generate a series of predictions at both phylogenetic and ontogenetic levels, despite the fact that it does not detail the exact proximate input-output relationships that lead to the developmental emergence of self-conception.

A key difficulty in detailing the predictions that derive from our model involves the issue of canalization. It is not clear to what extent the epigenetic system governing the construction of the psychological capacities in question is tightly canalized, and thus relatively impervious to rearing conditions. This issue is important because it ultimately affects the nature of the tests (described below) of our model. If the underlying neurobiological systems in question develop only as the result of specific proximate stimulations during complex locomotion during orangutan and chimpanzee ontogeny, then captive-reared animals might be expected to be quite different from feral-reared animals. We suspect that this is not the case, however. First, if our explanation of ultimate cause is correct, then humans no longer face the proximate challenges that led to the emergence of self-conception in the first place, yet they display the most robust forms of self-conception of all of the great apes. This suggests that the capacity in question can be canalized, as well as recruited and exploited in other (perhaps social) contexts. Second, many (but not all) captive chimpanzees do show expression of the capacities in question. The reason for individual differences remains

unknown, although many possibilities exist (Povinelli et al., 1993). Indeed, as we point out below, this individual variation may be quite relevant to our model.

Thus, although our model should be viewed as a somewhat preliminary description, as it is currently formulated it generates several predictions about the cognitive skills of the great apes and other nonhuman primates. Below we list these predictions, and the logic underlying them.

#### 1. LOCOMOTION AND SENSORIMOTOR INTELLIGENCE

The hypothesis that body weight-induced clambering led to the evolution of self-conception leads to several predictions concerning the relationship between sensorimotor intelligence and independent locomotion. In order to appreciate these predictions, it is necessary to review recent research concerning the relationship between the onset of locomotion and stage of sensorimotor intelligence in chimpanzees, gorillas and macaques. Antinucci (1989) and Potì and Spinozzi (1994) have both proposed that gorillas have undergone a heterochronic shift in the development of independent locomotion *vis-à-vis* sensorimotor intelligence. These researchers have collected data suggesting that gorillas, when compared to humans and chimpanzees, appear to begin to locomote in an earlier stage of sensorimotor intelligence. It is important to note that this relatively earlier form of independent locomotion leads to patterns of buccal prehension and decreased manipulatory tendencies in gorillas as compared to chimpanzees (Antinucci, 1989; Potì and Spinozzi, 1994). Ultimately, this results in gorillas appearing more similar to macaques in their pattern of sensorimotor development than to chimpanzees. Consistent with this argument, there is now mounting evidence from field studies that supports the proposition that the developmental schedules of gorillas (especially females) are distinctly accelerated compared to orangutans or chimpanzees (see Watts and Pusey, 1993). Arguments about the specific form of heterochronic changes that the various lineages have undergone depend crucially upon assumptions about the primitive character state, and at present are difficult to evaluate. The critical point

is that gorillas appear to be like macaques in terms of their locomotor development *vis-à-vis* sensorimotor intelligence, rather than being like orangutans and chimpanzees.

As noted earlier, Povinelli (1993, 1994) has proposed that such differences may have more long-lasting secondary consequences, which ultimately translate into phylogenetic differences in the expression of self-recognition in the great apes. In other words, it is possible that gorillas have secondarily masked the developmental construction of self-conception due to other changes in their development. Why might this be so? If gorillas have undergone a developmental shift in the timing of locomotion relative to sensorimotor intelligence, and if this is related to their general secondary precocial tendencies, then it is tempting to speculate that this is related to their secondary terrestrial adaptation. Thus, the typical failure of gorillas to show evidence of self-recognition could ultimately be traced to their readaptation to terrestriality. Chimpanzees, also, are secondarily adapted to terrestriality, but not to the same extent.

These series of assumptions allow us to predict that among the great apes, early locomotion relative to sensorimotor stages ought to be inversely correlated with degree of arboreality. In other words, we predict that the great apes showing the greatest degree of arboreality (orangutans) ought to be most delayed in locomotion relative to sensorimotor development. The central predictions to be derived from this hypothesis concern orangutans and bonobos, neither of which has been investigated for their degree of independent locomotion at given sensorimotor stages. Based on their degree of arboreality, our model predicts a rank order as follows: orangutans, bonobos, chimpanzees, lowland gorillas, mountain gorillas.

At present, there is insufficient evidence to support or refute the predictions. Captive chimpanzees, orangutans and gorillas have all been studied for their patterns of sensorimotor development (Chevalier-Skolnikoff, 1977, 1983; Redshaw, 1978; Vaclair and Bard, 1983; Bard, 1990). There is some evidence that chimpanzees and orangutans do, in fact, pass through the first four sensorimotor stages faster than gorillas during development (Chevalier-Skolnikoff, 1983); however, the most

detailed data are inconsistent, and primarily derived from animals in captivity. More importantly, our prediction concerns locomotion relative to sensorimotor intelligence, and so far data on this exist only for a single captive gorilla and several captive chimpanzees. No one has yet studied the sensorimotor stage at which orangutans begin to locomote independently, although Bard (1987) has examined the sensorimotor development that takes place after the establishment of locomotor competence in free-ranging orangutans. Clearly, longitudinal developmental studies of both captive and feral chimpanzees, gorillas and orangutans are needed to test our predictions.

Humans represent an obvious and important exception to our general thesis that degree of arboreality ought to be inversely correlated to relative age of independent locomotion. Humans are completely terrestrial, yet they do not locomote independently until Stage 5 of sensorimotor intelligence. There may be several reasons for this, but most importantly humans have become extremely altricial in physical maturation, presumably due to selection for increased brain size at birth. This altriciality results in the birth of a comparatively helpless infant. The result may be an absolute delay of independent locomotion, which, if sensorimotor development is held constant, may automatically cause infants to locomote in later stages of sensorimotor intelligence.

## 2. ONTOGENY OF SELF-RECOGNITION

Since our model tacitly accepts self-recognition as an empirical marker of the onset of a form of self-conception, it allows us to advance a prediction concerning developmental differences among those apes that display self-recognition (orangutans, chimpanzees, and, presumably, bonobos). We predict that orangutans ought to show self-recognition at an earlier age than chimpanzees. This prediction can be derived from an examination of the potential locomotion conflict between orangutan mothers and infants. It seems reasonable that because the weight of a dependent infant will add to a female orangutan's difficulty in negotiating its arboreal habitat, it is in the female's interests to have the infant achieve locomotor independence as early as possible. The infant's

interests run in the opposite direction, however, because physical and cognitive immaturity make it difficult to follow the pathways traversed by the mother.

If our model is correct, the potential benefit to the female will only translate into an evolutionary benefit if its infant ultimately develops the kinds of psychological mechanisms we have described for negotiating the habitat. As explained above, this seems to require infants to delay the onset of locomotion relative to sensorimotor intelligence, potentially delaying the age at which they locomote independently, and heightening the mother-infant conflict described above. This conflict could be reduced, however, if orangutan infants either compressed the absolute length of their early sensorimotor stages into a shorter time span, or conversely, retained a smaller body weight for a longer period of time. In the former case, selection would favor variants who expressed an absolutely faster rate of early sensorimotor development. Mothers could still achieve early body weight independence from their offspring, and infants could still delay locomotion relative to sensorimotor intelligence. Thus, it can be predicted that orangutans should have an absolutely faster rate of sensorimotor development than the other apes, up until the stage at which they achieve locomotor independence (probably toward the end of Stage 3 or beginning of Stage 4). After that point, our model is silent on whether sensorimotor intelligence may be presumed to remain similar to the ancestral condition, or faster, or slower. Because there is no reason to expect otherwise, we conservatively predict that the rates of sensorimotor development after locomotor independence should be more or less constant across the species of apes. In the latter case, selection would maintain slow body weight growth curves for orangutan infants until the end of sensorimotor intelligence.

The predictions for self-recognition can be derived from the above logic. On the one hand, orangutans can be predicted to show slightly faster rates of the first few stages of sensorimotor development than the other great apes, but to begin to locomote in a later stage. In human infants, self-recognition emerges between 18–24 months of age, possibly coincident with the achievement of stage

6 of sensorimotor intelligence (for example, stage 6 object permanence, Bertenthal and Fischer, 1978). Thus, if selection has placed a premium on rapid advancement through the first three stages of sensorimotor intelligence in orangutans, and if after that point they proceed at the same rate as the other apes, orangutans ought to show absolutely earlier development of self-recognition than either chimpanzees or bonobos. Typically gorillas, of course, do not develop the capacity for self-recognition. On the other hand, orangutans may take almost as long to pass through the sensorimotor stages, but maintain low infant body weight. In this case, our model predicts that rapid weight gain ought to coincide with the closure of sensorimotor intelligence, and hence the onset of self-recognition.

Unfortunately, very little is presently known about the ontogeny of self-recognition in chimpanzees and orangutans. The research that has been reported to date suffers from a variety of methodological problems (e.g., Hill et al., 1970; Robert, 1986; Lin et al., 1992). Recent research with over 100 chimpanzees suggests that self-recognition may be markedly delayed in chimpanzees as compared to human infants (Povinelli et al., 1993; Eddy et al., in press). Indeed, it is of great interest to us that this new research suggests that many chimpanzees do not develop self-recognition until about 4.5 to 8 years of age, precisely the point at which most previous investigators have discovered the close of Stage 6 sensorimotor development in chimpanzees (see Chevalier-Skolnikoff, 1983). In addition, this is the same age (5 to 8 years) that Bard (1987) reported the most complex forms of sensorimotor intelligence (planning in advance of acting) being used by feral orangutan juveniles during complex bouts of locomotion. This would tentatively appear to support the second possibility outlined above, namely, that orangutan infants ought to show modest growth until the approximate age at which self-conception develops.

Clearly, laboratory approaches are needed to test this prediction, but to the extent that the environmental conditions in which an animal is reared affects early cognitive and physical development, the interpretation of results will be compromised.

### 3. POPULATIONAL DISTRIBUTIONS OF SELF-RECOGNITION

An obvious corollary of our model is that in those species that have deviated from the ancestral ecological conditions that led to the need for self-conception in the first place, selection may not be maintaining the trait as rigidly as in the past. Thus we can predict that within-species variation in both the emergence and maintenance of the trait ought to be far greater in those species that have become secondarily terrestrial. So, a greater percentage of orangutans ought to show evidence of self-recognition than chimpanzees. Indeed, selection might be thought to be acting not only upon the initial development of the capacity, but upon its subsequent retention as well. Orangutans, who will need their clambering skills throughout their lives, may be under selection to maintain the trait throughout development. This is consistent with recent evidence suggesting a decline in self-recognition in adulthood in captive chimpanzees (see Povinelli et al., 1993). Indeed, viewed from this perspective, gorilla populations may just be a special case, with drift (coupled with selection for earlier physical maturation) having reduced the number of individuals retaining the trait to very few, or none, despite the fact that they retain the latent capacity to develop the trait. In a different context, Gallup (personal communication, 1986) suggested that the differences between gorillas on the one hand, and orangutans and chimpanzees on the other, in terms of self-recognition, might be due to differences within populations. Our model provides a theoretical explanation for his conjecture.

### 4. TASKS OF PERSONAL AGENCY

If we are correct that body weight-induced clambering has driven the evolution of a sense of personal agency, and that this psychological capacity supports the behavior of self-recognition, then the phyletic differences in self-recognition ought to predict phyletic differences in the sense of personal agency. Thus, on tasks that require an organism to demonstrate a sense of personal agency, chimpanzees and orangutans ought to perform quite well, whereas gorillas should perform poorly. At least one such nonverbal task involving the ability to

reverse social roles has been used successfully in comparisons between rhesus macaques and chimpanzees (Povinelli et al., 1992a, 1992b; Hess et al., 1993). Admittedly, this prediction is also made by Gallup (1982, 1985), but our model allows for a further prediction, unanticipated by that framework. We predict that among those species capable of self-recognition, those that still employ a high degree of body weight-induced clambering ought to show a more robust and more complex understanding of themselves as causal agents. Thus, orangutans, although at a greater phylogenetic distance from humans than are chimpanzees, ought to resemble humans more closely in this domain. To the extent that they turn out to do more arboreal clambering, bonobos should follow next, with chimpanzees relatively more distant. Gorillas, because of their inability to recognize themselves, would not be expected to show evidence for such an ability in the first place (see Gallup, 1982).

### 5. STATES OF OBJECTIVE SELF-AWARENESS

Because our model argues that a sense of personal agency, and hence self-conception, emerged in the context of locomotion, we can predict that for organisms that are capable of self-conception, engaging in nonstereotyped locomotion ought to induce states of "objective self-awareness" (Duval and Wicklund, 1972). These authors argued for a distinction between "objective" and "subjective" states of self-awareness, where objective self-awareness corresponds to states in which an individual has its attention focused inward upon its own mental experiences and/or personality traits, and where "subjective self-awareness" corresponds to states in which the individual's attention is focused outward on objects or events in the external world. Duval and Wicklund's ideas have stimulated a variety of empirical investigations. Researchers have shown that these different states can be induced by simple experimental manipulations, as well documenting how individual variation in the amount of time people spend in such states influences their behavior. For example, states of objective self-awareness can be induced by having a subject wear a large name-tag, or point to themselves, or confront themselves in a mirror. These findings are of

interest, because it can be empirically demonstrated that people confronted with identical situations will behave differently, depending upon whether a state of objective self-awareness has been previously induced (reviews by Wicklund, 1975; Carver, 1979).

This approach to understanding the self allows us to predict that performing nonstereotyped locomotor behaviors should induce states of objective self-awareness in humans, chimpanzees, and orangutans (in much the same way that mirrors do), but not gorillas, gibbons, macaques and other primates. Forcing subjects to cope with locomotor situations in which their stereotyped action schemata are no longer sufficient should induce a state of inward assessment and evaluation as the subject determines possible options for moving through the environment. Examples of the types of dependent measures that can be used to assess the presence or absence of states of objective self-awareness are widely available in the literature. Adapting these procedures for use with nonverbal nonhuman primates is a difficult problem, but following Premack and Woodruff's (1978) lead, it is not impossible (see also, Premack, 1988; Premack and Dasser, 1991; Povinelli, 1993, for discussions of construction and validation of such tasks).

#### SUMMARY AND CONCLUSIONS

Existing frameworks for understanding the evolution of primate intelligence do not explain the apparently unique forms of intelligence restricted to the great ape/human clade. We hypothesize that heavy body weight, coupled with a commitment to an arboreal lifestyle, led to the emergence of a limited self-concept in the ancestors of the great apes and humans as part of a mechanism for planning

and executing unusually complicated forms of locomotion. This understanding of the self as a causal agent presupposes the concurrent emergence of the capacity to conceive of the self in the first place. Our model explains— from an evolutionary perspective— why behaviors related to self-conception (e.g., self-recognition) appear to be limited to only the large-bodied apes and humans. More importantly, the model also generates a number of falsifiable predictions that can be tested by using a combination of field and laboratory approaches.

It was once believed that the origin of complex “human-like” mental faculties awaited our ancestors' descent from the trees and their subsequent evolution of an enlarged brain, upright posture, tool use, language, and cooperative gathering and hunting. We do not dispute these factors as playing an essential role in the evolution of human intelligence and material culture. Nevertheless, we hypothesize that a major turning point—the origin of self-conception— occurred as the result of our ancestors' “decision” to remain in the trees long after their body size favored descent.

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