

Bodily Origins of SELF

Jochen Barth

Max Plank Institute for Evolutionary Anthropology

Daniel J. Povinelli

University of Louisiana at Lafayette

&

John G.H. Cant

University of Puerto Rico

Thirty-five years ago, Gallup (1970) reported the existence of a surprising phylogenetic difference in the capacity of organisms to recognize themselves in mirrors: the ability appeared to be present in chimpanzees, but not in several species of monkeys that he tested. After being exposed to mirrors, he observed chimpanzees apparently using their reflected images to explore parts of themselves that they had never had the opportunity to see before (their eyes, teeth, nose, and ano-genital area, for example). Figure 1 provides some examples of these behaviors captured in our own laboratory. To confirm the interpretation of these spontaneous reactions, the chimpanzees were anesthetized and surreptitiously marked with a red dye on the upper portion of their eye brow ridge and ear (locations that

were only visible with the aid of a mirror). Upon recovery, the chimpanzees made no attempt to touch these areas until they were again allowed to observe themselves in a mirror, at which point they immediately began touching the marked regions of their faces (see also Povinelli et al., 1997). Gallup concluded that the chimpanzees had learned to recognize themselves in mirrors. Gallup (1970) also tested several species of Old World monkeys using the same procedures. Surprisingly, the monkeys, although initially interested in the mirror, neither exhibited the self-exploratory behavior, nor touched the red spots on their faces during the mark test.

Reports from a number of laboratories replicated Gallup's (1970) findings with chimpanzees, and continued to fail to find evidence for mirror self-recognition in lesser apes and a wide array of other non-human primates (review by Anderson & Gallup, 1999). Other research extended the presence of the capacity for mirror self-recognition to another great ape species, orangutans, but somewhat surprisingly, not gorillas (e.g., Suarez & Gallup, 1981). More recently, the final species of great ape, bonobos (*Pan paniscus*) has been tested and reported to exhibit evidence for mirror self-recognition, as well (although these latter tests have lacked important controls; Hyatt & Hopkins, 1994; Walraven, Elsacker & Verheyen, 1995).

The Body in the Mirror

As time passed, and evidence continued to suggest a robust difference in the capacity for self-recognition in mirrors between chimpanzees, orangutans and humans, on the one hand, and other primates on the other, Gallup (e.g., 1977) increasingly favored the provocative conclusion that differences in the capacity of organisms to recognize themselves in mirrors might reflect differences in the presence of self-awareness, what he defined as the ability to

become the object of one's own attention. His common-sense interpretation of the results was that it was impossible to know who it was you were seeing in a mirror unless you first had a concept of self. Later, Gallup (1982) further speculated that if chimpanzees and orangutans were self-aware in this sense, they might also have the capacity to reflect upon their own experiences and, by inference, the experiences of others as well.

Gallup's empirical findings concerning the phylogenetic distribution of the phenomenon of mirror self-recognition have withstood the test of time (see below, and recent review by Anderson & Gallup, 1999). However, until recently, the accounts of why these kinds of reactions to seeing the self in a mirror were restricted to chimpanzees, orangutans and humans were sparse (and troubling) – as were detailed theories of the cognitive mechanisms supporting the ability. On the face of it, the fact that this ability was limited to the great apes and humans seemed odd, especially given the difficulty of imagining an ecological context in which evolution would have favored the ability to recognize oneself in a mirror. Rather, self-recognition in mirrors was seen as a byproduct of selection for some other, unspecified abilities (e.g., Humphrey, 1976). Reasoning in this manner, some scholars attempted to link the phenomenon with a higher degree of social intelligence, but this account left unexplained why the ability was not found in the dozens of other highly social primates, but was present in highly solitary orangutans.

The first integrated evolutionary account of why the capacity for self-recognition in mirrors was restricted to the great apes and humans was provided a decade ago by Povinelli and Cant (1995). Their explanation took a surprising turn, essentially amounting to an account (contra ideas by Gallup, 1982) of how the great apes evolved a more explicit representation of their *bodies*, not their minds. Povinelli and Cant argued that the unique

aspects of the self-concept that evolved in the ancestor of the great apes and humans (aspects that are reflected in the mirror test), were largely *kinesthetic* ones (see Gallup, 1970). They speculated that an explicit representation of some aspect of the kinesthetic component of the self evolved as a result of a peculiar convergence of organismal and ecological factors faced by the common ancestor of the great apes and humans. In particular, they hypothesized that the four-fold difference in the body mass of the great apes (chimpanzees, bonobos, orangutans, and gorillas) as compared to other highly arboreal (tree-dwelling) primates, generated substantial challenges for these animals as they evolved their larger body masses. Povinelli and Cant proposed that this evolutionary increase in body mass rendered the habitat increasingly difficult to traverse, primarily because of the severe deformation of supports (tree limbs) caused by this body mass. Using aspects of the morphology and behavior of modern orangutans as a rough model of the common ancestor, they highlighted how the orangutan's extreme body mass forces it to spend a non-trivial amount of time engaged in locomotor activities that appear to require a great deal of flexibility and planning in the translocation of the body through the arboreal habitat in which it travels. Finally, they speculated that this process of locomotion required the co-evolution of a more elaborated representation of the body and its actions to assist in planning and deploying its movements. For purposes of clarity, we shall hereafter refer to this particular body-image¹ and its attendant systems as 'SELF' (Self Evolved for

¹ We use the term 'body image' in connection with the conceptual system that evolved in response to selection for a more explicit, conceptual representation of the body and its movements (i.e., the SELF system) that evolved in the ancestor of the great apes and humans. In subsuming the SELF system under the umbrella of the concept of the 'body image', we attempt to follow the standard convention in distinguishing between the concepts of 'body image' and 'body schema' (see, for example, Gallagher, 1986). Although we are not fully comfortable with that distinction as applied here, if one of the central distinctions between 'body image' and 'body schema' is that the former is a conceptual structure whereas the latter is not, then the SELF system,

Locomotor Flexibility in large-bodied arboreal primates in highly compliant environments; or ‘SELF’ for short). Povinelli and Cant further speculated that this self-representational system might have established a quite explicit self concept, one which allows for the behaviors characteristic of mirror self-recognition, and one which may have served as the point of departure for the more elaborate, psychological aspects of the self-concept so characteristic of humans. In this chapter, we re-visit this model, and clarify and refine certain of its features. We also offer suggestions for new research directions, along with some preliminary investigations we have conducted to test certain ideas that can be derived from our model.

We begin by reviewing the current evidence concerning species differences in mirror self-recognition. We then provide a brief account of a class of causal models of the phenomenon, and show why self-recognition in mirrors may depend, fundamentally, upon an explicit, kinesthetic representation of the self (SELF) which initially evolved to subservise behavioral solutions to the problems created by the large body mass that evolved in the ancestor of the great apes and humans. Next, we explore the distribution of other abilities in chimpanzees and the great apes which may also either depend upon or be greatly facilitated by the SELF system purported to be uniquely present in these species. In doing so, we describe a preliminary attempt to test the generality of one component of the model by testing whether the SELF system of chimpanzees (and presumably orangutans, as well)

as we envision it, would fall under the rubric of ‘body image.’ One of the only other axes of contrast between ‘body image’ and ‘body schema’ in the human literature is the ‘conscious versus subconscious’

distinction – a dichotomy of little practical use in dealing with non-human primates. A more interesting point of theoretical difficulty is that ‘body schema’ is typically used when referring to unconscious systems that play a dynamic role in monitoring and governing posture and movement (e.g., Head, 1920).

expresses itself in situations other than mirror self-recognition (in this case, a tool-using situation).

A Short Course on Mirror Self-Recognition in Primates and Other Animals

Three challenges have been raised in response to Gallup's claim that mirror self-recognition is restricted to the great apes and humans: (1) chimpanzees do not really display the behaviors Gallup reported, (2) chimpanzees *do* exhibit these behaviors, but so do other non-human primate species (including gorillas and certain species of monkeys), and (3) regardless of whether other primates do or do not exhibit self-recognition, certain non-primate taxa (such as dolphins) can do so. We briefly examine each of these claims in turn.

Do chimpanzees 'recognize' themselves in mirrors? Yes

Gallup's (1970) interpretation of the spontaneous self-exploratory behaviors exhibited by chimpanzees (in conjunction with the subjects' responses to the marks tests) was that chimpanzees were capable of using mirrors to explore parts of their bodies that were not previously visible to them. In a widely circulated series of reports, Heyes (1994, 1995, 1998) challenged this (and other aspects) of Gallup's (1970) interpretation. She hypothesized that the spontaneous self-exploratory behaviors reported by Gallup and others were inherently ambiguous, and that the increase of mark-directed touches from the control to the test period could be explained in other ways. In particular, she argued that chimpanzees normally engage in a significant level of ambient face-touching behavior (e.g. scratching and self-grooming), and therefore speculated that a likely effect of the anesthesia used in the marking procedure would be to depress these baseline levels of face-touching

behaviors. She thus argued that the elevation in touches to the marked regions during the test period that Gallup (1970) and others have reported, may have been due to a decline in the effects of the anaesthetic agent across the control and test period. This amounted to a claim that the entire phenomenon of self-recognition in chimpanzees was a methodological artifact.

Povinelli et al. (1997) tested several competing predictions that can be derived from Heyes' model versus the self-recognition model, and in each case found clear and unambiguous support for the predictions of the self-recognition model. Indeed, the results were incompatible with every empirical prediction that can be derived from Heyes' model. First, during the mark tests, the chimpanzees selectively touched the marked areas of the face, as compared to the contralateral, unmarked areas (Figure 2). Second, unlike the pattern predicted by a gradual recovery from anesthesia (a gradual increase in touches to the marked areas of the face), there was a clear temporal spike in the chimpanzees' touches to the marked regions *coincident with the uncovering of the mirror* (see Figure 2). Finally, after spiking, the number of touches to the marks *declined* across the test (as opposed to increasing and stabilizing at some ambient level, as predicted by Heyes), presumably because the animals discovered their inconsequential nature (see Figure 2).

Although the predictions of Heyes' proposal have been empirically falsified, it should be noted that investigations with larger numbers of chimpanzees of different ages have suggested that certain qualifications of Gallup's (1970) original conclusions are nonetheless warranted. First, there is a much more rapid onset of self-recognition in mirror-naive animals than reported by Gallup (Povinelli et al., 1993). Second, there are developmental dissociations among some types of mirror-mediated, self-directed behaviors

and others (Povinelli et al., 1993; Eddy, Gallup, & Povinelli, 1996). Third, only certain types of mirror-mediated behaviors (e.g. self-exploratory behaviors) are associated with passing the mark test (Povinelli, Rulf, Landau, & Bierschwale, 1993; Eddy, Gallup, & Povinelli, 1996). And finally, not all chimpanzees exhibit behaviors diagnostic of self-recognition (Swartz & Evans, 1991; Povinelli et al., 1993; de Veer, van der Bos, Theall, Gallup, & Povinelli, 2002). None of these facts, however, suggests that the general phenomenon as reported by Gallup (1970) is not real. Indeed, test-retest measures have suggested stability of this trait in many individual animals for up to eight years (de Veer et al., 2002).

Is self-recognition absent in lesser apes and monkeys? Apparently so

Literally hundreds of monkeys, representing a wide array of species, have been tested in the 35 years since Gallup's (1970) original report (see Anderson & Gallup, 1999). Furthermore, the range of techniques that have been employed to try to 'pry' this capacity out of monkeys is impressive (see Anderson & Gallup, 1999), if for no other reason than that these attempts stand as a constant reminder that the phylogenetic difference in the capacity does not appear to be a trivial one. This is not to say that no one has claimed to have found the capacity in species of non-human primates outside the great ape/human group. Perhaps the most celebrated of these was a report by Hauser et al. (1995) who reported to have demonstrated self-recognition in virtually every cotton-top tamarin that they tested. However, after the original videotapes of this study were made available, and the methodology and interpretation of this study were criticized (e.g., Anderson & Gallup, 1997), the authors later reported a series of failures to replicate their results (Hauser, Miller, Liu, & Gupta, 2001).

Naturally, there are two ways of interpreting the inability to detect the capacity for self-recognition in primates outside the great ape/human group. One approach is to try to understand what this difference might mean about the self-representational systems of species (or individual organisms) which do and do not exhibit evidence of self-recognition in mirrors. The other approach is to assume that the differences that have been observed to date do not reflect significant, underlying cognitive differences among species, but instead are superficial artifacts of minor attentional, motivational, and/or perceptual differences. With respect to the latter strategy, numerous methodological explanations have been offered as possible reasons why monkeys do not display mirror-mediated self-exploratory behaviors or pass the mark test. In our estimation, however, none of these possibilities has survived empirical scrutiny (see Anderson & Gallup, 1999).

Let us briefly examine just two of the most frequently raised methodological concerns surrounding the empirical findings with monkeys. First, it has been widely suggested that because direct eye contact is typically a threatening signal in monkeys, they avoid closely inspecting their mirror images, and hence fail to learn as much about their mirror-image as do chimpanzees and orangutans (see, e.g., Gallup, Wallnau, & Suarez, 1980). A study by Anderson and Roeder (1989) examined this idea by confronting capuchin monkeys with two mirrors placed at a 60° angle to each other, thus allowing them to look at themselves without having to make direct eye contact. Despite extended exposure, the capuchins showed no evidence for mirror self-recognition (see also Anderson & Gallup, 1999, for other attempts to test this hypothesis).

Second, many skeptics have suggested that perhaps monkeys, lesser apes, and even gorillas, are simply not as interested in their bodies as are chimpanzees and orangutans.

Thus, perhaps they do not pass the mark test simply because they do not care about the appearance of these marks. Gallup, Wallnau, and Suarez (1980) tested this hypothesis by marking monkeys on their abdomens, as well as on their ears and forehead. Upon recovery from anesthesia, the monkeys exhibited an intense interest in touching and inspecting the marks on their abdomens (the ones they could directly see), but not the ones they could only observe through the mirror (the ones on their faces), thus ruling out the idea that they were simply uninterested in such marks. A similar study by Suarez and Gallup (1981) involving four gorillas exposed these animals to mirrors for a total of 80 hours. Despite this extended interaction with mirrors, these gorillas did not attempt to touch the experimentally applied marks on their faces during the mark test, even though they exhibited considerable interest in marks that were placed on their wrists (see also Shillito, Gallup, & Beck, 1999). This procedure has since emerged as an important motivational control for the mark test in species (or individuals) which do not exhibit evidence of self-recognition (e.g., Povinelli et al., 1993).

Are gorillas a puzzling case? Yes and no

Gallup's (1970) initial assumption was that the ability for self-recognition might be restricted to the great apes and humans. Extensive testing of gorillas, however, has revealed that these great apes typically do not exhibit the kinds of spontaneous self-exploratory behaviors in front of mirrors displayed by chimpanzees and orangutans, nor have they exhibited evidence of passing properly controlled² mark tests (see Suarez & Gallup, 1981;

² Three properly controlled tests have not elicited any evidence of self-recognition in gorillas (Suarez & Gallup, 1981; Ledbetter & Basen, 1982; Shillito, Gallup, & Beck, 1999), despite some rather extreme efforts to rule out methodological artifacts (see especially the report by Shillito et al., 1999). Despite this, there have been numerous claims for self-recognition in gorillas (see review by Swartz, Serauw, & Evans, 1999).

Ledbetter & Basen, 1982; Shillito, Gallup, & Beck, 1999). On the face of it, this should be puzzling, given the phylogenetic relationships of the great apes and humans (Figure 3). The orangutan lineage diverged earliest from the last common ancestor of this group, whereas chimpanzees, gorillas, and humans are more closely related. Given the presence of the ability in most species of great apes, but its absence in all other primate species tested thus far (see Figure 3), the most parsimonious analysis suggests that the capacity evolved in the last common ancestor of the great-ape/human group, and that this capacity was subsequently lost in the gorilla lineage (see Povinelli, 1994). Although the loss of this ability in gorillas may at first seem odd, as we discuss below, this fact turns out to be consistent with the evolutionary model offered by Povinelli and Cant (1995). In other words, the absence of self-recognition in mirrors in gorillas may be understandable in the context of the clambering hypothesis.

Can dolphins recognize themselves in mirrors? Maybe, maybe not

Numerous species outside the primate order have been assessed for their reactions to their mirror images (see Gallup, 1968, for a review), but only a handful of them have actually been tested using Gallup's (1970) procedure. Furthermore, until recently, none had been reported to exhibit patterns of behavior suggestive of self-recognition (e.g., elephants: Povinelli, 1989). An exception may be dolphins. Reiss and Marino (2001) reported positive evidence of 'self-directed' mirror-mediated behavior in two bottle-nosed dolphins, where 'self-directed' referred to elevations in the amount of time dolphins spent looking at

However, data supporting the existence of mirror self-recognition in gorillas are derived from tests that have not implemented key control procedures that are necessary in order to draw strong conclusions as to the presence or absence of the capacity (see Gallup, 1994, for a detailed discussion of the logic of various procedures). This is not to rule out the possibility that gorillas, under certain abnormal circumstances) could

themselves in mirrors, and the adoption of certain postures while marked. It is important to note, however, that the evidence for self-recognition in dolphins derives from measurements that are not strictly comparable to those used with primates. Two dolphins were repeatedly either marked or sham-marked (i.e., the experimenters merely pretended to mark them) while fully conscious. Dolphins were then reported to swim to a pre-existing mirror faster³ when they were marked (or sham-marked) and were reported to spend more time in front of a mirror when marked than when not marked. However, the fact that an organism may increase the amount of time spent looking in a mirror after having been marked does not necessarily indicate self-recognition. For example, over 20 years ago, Gallup and his colleagues showed that rhesus monkeys will exhibit elevated levels of looking at a mirror after having been marked without exhibiting spontaneous self-exploratory behavior or attempting to touch the marks on their face (e.g., Gallup, Wallnau, & Suarez, 1980). It is as if the monkey in the mirror has become interesting again because of the novelty of its marked face! Nonetheless, despite the reservations we have expressed here, if the findings of Reiss and Marino (2001) are replicated with a design that surmounts the interpretative problems we have expressed, the capacity for self-recognition in dolphins

exhibit evidence of self-recognition (see Povinelli, 1994), but thus far the best evidence suggests that normally-reared, socially housed gorillas do not.

³ One dolphin was also reported to expose the part of its body that had been marked as the first behavior when it reached the mirror, but this was only true in 6/8 cases, with 2 cases excluded because they were ambiguous. If the 2 ambiguous cases are included as negative instances, this would constitute only 6/10 cases. Because no data concerning how unmarked dolphins typically present their body to a mirror was provided, it is not clear how to compare these data to a baseline performance. The authors also stress the fact that the same dolphin exhibited no social behavior to the mirrors. However, as the authors themselves note, the subjects were thoroughly habituated to the mirrored surfaces in their tanks. Finally, the authors also report that no social behavior was observed when mirrors were reintroduced. Unfortunately, no systematic data appears to have been collected to support this point. In any event, although the presence or absence of social behavior to mirrors has been speculated to be related to self-exploratory behaviors (e.g., Suarez & Gallup, 1986), empirical data suggests that this measure does not predict whether chimpanzees exhibit evidence of self-recognition (see Povinelli, Rulf, Bierschwale, & Landau, 1993).

would constitute a remarkable case of convergent evolution, and could point to an alternative evolutionary route for evolving a SELF system.

Body Mass, Habitat Deformation, and the Evolution of SELF

With respect to the phylogenetic distribution of the capacity for self-recognition in mirrors, the evidence just reviewed continues to point in the direction suggested by Gallup over three decades ago: spontaneous, mirror-mediated, self-exploratory patterns of behavior, and positive results using the mark test, appear to be limited to the great apes and humans (with the caveats concerning gorillas and dolphins described above). This means that 15-20 million years ago, some ability evolved in the common ancestor of the great apes and humans that now manifests itself as the capacity for self-recognition in mirrors. But what exactly was this ability, and what was the evolutionary context that produced it? Any attempt to answer this question must begin by providing a clearer specification of what the task is measuring in the first place.

Theory of the mirror self-recognition task

As his thinking about the task developed, Gallup (e.g., 1977) increasingly assumed that the patterns of behavior exhibited by chimpanzees in front of mirrors are generated by an inference of the sort, “That’s me!” But what dimensions of ‘me’ must necessarily be represented in order to respond to mirrors in this way? Gallup (1982, 1985, 1998) has emphasized the role of reflecting on one’s own mental states. Further, he and others have suggested that the capacity for self-recognition in mirrors in both human infants and chimpanzees may be connected with the emergence of an objective perspective on the self’s past and future, by attempting to link the onset of self-recognition in human toddlers (occurring at around 18-24 months of age) with the emergence of autobiographical memory

(see Brooks-Gunn & Lewis, 1984; Gallup, 1982, 1998; Howe & Courage, 1993, 1997; Howe, this volume).

But do the behaviors exhibited by chimpanzees and young children in front of mirrors really depend upon representing these psychological and temporal dimensions of the self? Both Mitchell (1993) and Povinelli (1995) have each offered alternatives to these views, and have provided detailed analyses of the mirror task which suggest that mirror-mediated self-exploratory behavior (including passing the mark test) may most directly depend on an explicit representation of one's kinesthetic states – one's body image. Indeed, this general idea seems consistent with Gallup's (1970) original view of the task:

“... self-directed and mark-directed behaviors would seem to require the ability to project, as it were, proprioceptive information and kinesthetic feedback onto the reflected visual image so as to coordinate the appropriate visually guided movements via the mirror” (p. 87). However, the exact mechanisms by which infants (and chimpanzees) come to understand the explicit connection between their body and their mirror image has been a matter of some debate, with several theories currently on the table for consideration. In order to gain some insight into the nature of the self-representation that may have evolved in the last common ancestor of the great apes and humans, it is necessary to briefly explore causal theories of the phenomenon of mirror self-recognition in humans.

Mitchell (1993) has argued that the young child (or chimpanzee, for that matter) must first learn that mirrors contingently reflect objects in front of them before they can apply this idea to the case of their own body, and has offered two theories about how this might be accomplished. The existing data would seem to suggest that this premise is incorrect; it is not necessary to understand how mirrors work in order to pass the mark test

(discussion by Povinelli, 1995). Research with human infants, for example, has consistently shown that there is no correlation between whether infants pass the mark test and whether they can solve a simple task of turning around to look at a toy that is presented in a mirror (Loveland, 1986; Robinson, Connell, McKenzie, & Day, 1990). Thus, passing the mark test would not seem to depend upon understanding the pragmatics of mirror use. Further, human infants raised in cultures without mirrors pass the mark test at the same age as infants raised in cultures with mirrors, after only a brief (5-minute) pre-test exposure to their mirror image (Priel & de Schonen, 1986).

Povinelli's (1995) theory of self-recognition in human infants also emphasizes the role of the kinesthetic dimension of the self, but, unlike Mitchell's theory, specifies that understanding the pragmatics of how mirrors work is not necessary to exhibit patterns of self-exploratory behavior, or to pass a mark test. Instead, his theory pinpoints the existence of an explicit representation of the integrated body image as the critical factor. Once an organism can hold in mind a representation of the current state of its body, it is in the position to begin to form explicit relations among objects of perception (e.g., the image in a mirror) and the body image. One such relation that seems critical to exhibit the patterns of behavior that are taken to be criterial for self-recognition in mirrors, is an equivalence relation: *That thing (image in the mirror) is equivalent to my body.*⁴ In analyzing the mirror task, Gallup (1970), Mitchell (1993), and others have emphasized the role of a system that

⁴ We concede that the presence of the notion of the possession of the body (implied here by the phrase 'my body', as opposed to 'this body'), raises difficult philosophical problems which we do pretend to have solved (see, for example, Martin, 1995). With respect to the mirror task, Davis (1989) has provided a detailed analysis of the minimal kind of self-concept that needs to be ascribed to the organism that passes it. He concludes that the test at least demonstrates the existence of a concept of 'my body' that includes material properties (color, shape, contour, texture, location, movement, etc.).

matches (commonly codes) kinesthetic and visual information. While not denying the role that such common coding must play in the self-recognition task, Povinelli has noted that various forms of imitation are present well before 18 months, some even at birth (see Meltzoff & Moore, 1999, for a review). Therefore, such systems are not likely to be the limiting factor for the self-recognition task.

The above considerations can be interpreted to suggest that a crucial advance in the development in self-representation in human infants occurs when the kinesthetic aspect of the body is raised to a level of explicitness that it can be held in mind as an object of attention in its own right (Povinelli, 1995). This kind of ‘on-line’ representation of the self’s bodily actions can be contrasted with an even more advanced understanding of the self as a thing that has repeated instantiations across time – a continuous history.

The present self, extended in time

Since the early 1990s, Povinelli and colleagues have been attempting to better understand the kind of on-line, kinesthetic self-representation supporting mirror self-recognition in human infants, by contrasting it with a more temporally extended self-representation that emerges later in development (see Povinelli, 2001, for a review of this research). In one extended series of studies, they explored the role that temporal contingency plays in supporting mirror self-recognition in young children. For example, when the images observed by the young child were not live (as they are in a mirror) but slightly delayed, this strongly affected the children’s ability to exhibit evidence of ‘recognizing themselves.’ In one series of studies, Povinelli, Landau, and Perilloux (1996) exposed 2-, 3- and 4-year-old children to both live and briefly delayed visual images of themselves. In one experiment, each child was videotaped as he or she played a distinctive

and novel game with an experimenter. During the game, the experimenter praised the child, and used this as the opportunity to secretly place a large, brightly-colored sticker on top of the child's head. Three minutes later, the children were either shown the video recording of the events that had just happened- including a clear depiction of the experimenter placing the sticker on their head. The results were striking. None of the 2-year-olds, and only 25% of the 3-year-olds reached up to search for the sticker. Although it might be tempting to think that the children simply did not notice the sticker in the delayed video, this was not the case. Many of them spontaneously commented or laughed when the video depicted the sticker being placed on their head. Furthermore, after the video playback was over, we drew their attention to the sticker on their image in the video, and asked them, "What is that?" The majority of the children responded, "It's a sticker", or something comparable. But significantly, this did not lead them to reach up to their own head to search for it. Even when we asked them if they could get it, they typically looked at the image, shrugged their shoulders and replied, "I can't." In another experiment, the same basic procedures were used to directly compare how 2–3-year-old children would react to seeing themselves in the standard delayed image, versus a live image. Most of the children in the live condition reached up to remove the sticker, whereas very few children in the delayed condition did so.

We must be careful here. In one sense, 2–3-year-old children can 'recognize themselves' in delayed video or photographs. For example, when asked, "Who is that?", even the youngest of preschoolers we tested replied, "me!" or stated their proper name (see Povinelli et al., 1996, Exp. 2; Povinelli & Simon, 1998; Povinelli et al., 1999, Exp. 1). However, this recognition seems to occur at the level of their physical features (perhaps

most strongly their facial features). For example, when asked, "Where is that sticker?" they frequently made reference to the 'other' child: "It's on *her* [or *his*] head." It was as if the children were saying, "Yes, that *looks* like me, but it's not *me* – she's not doing what I'm doing." One 3-year-old girl summarized this psychological conflict quite succinctly: "It's Jennifer," she stated – but then hurriedly added, "Why is she wearing my shirt?" Coupled with the results of the mark test, our conclusion from these data is that at any given moment, there are multiple dimensions of the self that might or might not be explicitly represented or 'recognized', and it should not be surprising that at various points in development not all of these aspects of the self may be available to the child.

So when does the child develop a more autobiographical or historical stance toward the self? Our tests reveal that by about 4 years of age a significant majority of children begin to pass our tests of delayed self-recognition, implying that they understand the historical-causal linkage between past and present versions of themselves. Unlike their younger counterparts, 4- to 5-year-olds typically reach up to remove the sticker when they observe the delayed images of themselves. Also, no longer do they refer to 'him' or 'her' when talking about the image, nor do they state their proper name. The transition in performance on our test at 4 years of age is generally consistent with the suggestions by Nelson (1992), Fivush (2001), Welch-Ross (1999), and others, that autobiographical memory may not emerge until 3.5- to 4.5 years of age – considerably later than the 18–24-month mark that others have suggested based in large part on the age at which children begin to recognize themselves in mirrors (e.g., Gallup, 1998; Brooks-Gunn & Lewis, 1984; Howe & Courage, 1993, 1997).

Perhaps the most dramatic confirmation of our interpretation of the delayed self-recognition tests came from a study in which we invited 3-, 4- and 5-year-old children to visit our center twice, with each visit separated by a week (see Povinelli & Simon, 1998). During the first visit, each child played a novel, distinctive game in a playroom with two experimenters. As in our previous studies, we secretly placed a sticker on their heads. However, at the end of the game, rather than letting them watch the video, we surreptitiously removed the sticker and the child went home. On the second visit, the child played a different game in a different room, during which we once again placed a sticker on his or her head. At this point, the critical manipulation of the study occurred: half of the children in each age group were shown the video recording of what had just happened, whereas the other half were shown the video from one week earlier. The 4- and 5-year-old children understood the difference. In these age groups, the children who saw the briefly delayed video reached up to their heads to search for the sticker, whereas the ones who viewed the week-old tape did not (see Figure 4). In direct contrast, not only did the 3-year-olds reach up less than half of the time, they did so with equal frequency whether they had been shown the 3-minute-old video or the week-old one (see Figure 4). Apparently, not only did the younger children generally not appreciate that the delayed images could be relevant to their current appearance, even the ones who did reach up to their heads did not take into account the critical variable: when the events had occurred in causal relation to the present moment.

Summary of the self-system that underwrites the mirror task

To recap, our theory of the mirror task is that the behaviors which are taken as evidence of ‘self-recognition’ in chimpanzees and very young children are supported by an

explicit mental representation of the actions of their bodies (possibly their agency) – not their mental states. We have argued that the mirror-mediated behaviors exhibited by chimpanzees and orangutans on the one hand, and young children, on the other, are, at their foundation, derived from an ability to form an explicit equivalence relation between what they see in the mirror and what they directly experience in their own behavior. Every time they act, the mirror (or live video) acts with them. An organism possessing an explicit representation (a concept, as it were) of this kinesthetic experience, ought to be able to conclude that "Everything that's true of this (my body) is also true of that (the mirror image) – and vice versa." Thus, unlike other species, chimpanzees and orangutans may possess an explicit or integrated enough representation of their bodies to have a concept ('my body') onto which they can map what they see occurring in a mirror. Note that this is not meant to imply that for 18–24-month-old human children the *only* aspect of the self explicitly represented is the body; rather, it is simply meant to suggest that regardless of whether other aspects of the self (say, the mental aspects) are represented or not, these other representations would not appear to play a pivotal role in eliciting behaviors diagnostic of passing the mirror test. From this perspective, the fact that in human infants the capacity for self-recognition in mirrors is correlated with certain kinds of knowledge of the psychological linkages between self and others, such as those underpinning the self-conscious emotions, synchronic imitation, and empathy (Asendorpf & Baudonniere, 1993; Bischof-Köhler, 1988; Lewis, Sullivan, Stanger & Weiss, 1989; Johnson, 1982) is all the more intriguing, because it suggests that in human development, at least, this level of explicitness of the self's physical aspect is linked in important ways to other kinds of

equivalencies between self and other. Whether these equivalences are present in the same fashion in other species that exhibit evidence of self-recognition in mirrors, such as chimpanzees, remains unclear.

Evolutionary origins of SELF: A body too heavy for the trees?

But then why do humans, chimpanzees and orangutans possess this integrated and explicit bodily self-concept in the first place, while other animals — such as monkeys — do not? This question amounts to asking what evolutionary forces sculpted this bodily representation in the last common ancestor of the great ape/human group.

Clearly, any viable theory of the evolution of the kind of body image that we are talking about must begin with the recognition that all organisms with a reasonably developed nervous system must possess dedicated systems for monitoring the effects of external stimuli on the body. In the case of organisms with complex central nervous systems, quite elaborated mechanisms for proprioceptive and kinesthetic feedback are present (see Berlucchi & Aglioti, 1997). This includes, of course, human infants (for discussions of the ‘ecological’ self of human infants, see Butterworth, 1992, 1995). Furthermore, it stands to reason that specific proprioceptive and kinesthetic systems are differentially elaborated in different lineages. However, there would seem to be no a priori reason why these aspects of the self would necessarily need to be represented as objects of knowledge in the central cognitive system in order to function effectively. (Indeed, for what it is worth, such systems are typically taxonomized under the construct of the ‘body schema’, and therefore placed outside the purview of the system of intentional action; see Gallagher, 1995.)

Thus, to make progress, we must be prepared to accept a distinction between systems which *embody* proprioceptive and kinesthetic information – that is, systems which are self-specifying for bodily senses – versus systems which *represent the body as an object* in its own right (akin to the distinction between ‘self-perception’ and ‘self-conception’; see Butterworth, 1992). With this distinction in mind, we need to ask, What factors could have led to the selection for a more robust and integrated representation of the body? or, Why would the ancestors of the great ape/human group, in particular, have needed to evolve a greater capacity to reason about the ongoing effects of the body on the environment during locomotion? As noted earlier, Povinelli and Cant (1995) proposed that this system – what we have for purposes of convenience and clarity labeled the SELF system – evolved to cope with a specific set of organismal and ecological factors that converged in the ancestors of the great apes and humans.

One clue as to why such an explicit representation of the body might have evolved when it did, lies in the large difference in body mass between the great apes and other primates. Consider orangutans, whose body mass and arboreal lifestyle may represent the closest living approximation to the condition of the last common ancestor of the great apes and humans. Povinelli and Cant (1995) noted that these 40 kg (female) to 80 kg (male) animals face specific problems in moving from one location to another that are not faced to an appreciable degree by other arboreal primates with smaller body masses. For example, as orangutans attempt to cross from one tree to the next, they not only encounter natural gaps in the canopy, but, due to their extreme body mass acting to deform the limbs of trees, they create gaps, as well. Of course, as any arboreal animal moves outward from the center of a tree, its body mass can, depending on the morphology of the branches, deform the

habitat around it, opening gaps between adjacent habitat structures. However, the deformation caused by the very large body mass of orangutans (especially adults) as they attempt to move from one resource patch to the next, creates unusually severe problems because, unlike smaller-bodied arboreal primates, the gaps they create are likely to be larger, and they cannot simply leap across such gaps (in fact, orangutans do not leap at all). Thus, what might be a more or less continuous path for a primate of smaller body mass (punctuated by gaps that they can leap across), will be experienced as a discontinuous path for the orangutan. We also suggest that the combination of the greater deformation caused by greater body mass with variable spatial arrangements of branches and lianas (themselves varying in compliance), create greater diversity of gap-crossing challenges for very large animals. Finally, because the relative strength of the habitat is reduced as body mass increases, and each support is less stable as it deforms downward, orangutans must be more selective about the structures they utilize. In summary, we propose that the different nature of discontinuity in the canopy for an arboreal mammal of very large mass, coupled with a general reduction in relative habitat strength and stability, combine to create unique challenges to effective locomotion. Thus an evolutionary increase in one dimension of the animal's body – its mass – has had cascading effects on its locomotion-related activities.

Reflecting on the interacting factors just discussed, Povinelli and Cant (1995) hypothesized that the dramatic increase in body mass that occurred during the evolution of the ancestor of the modern great apes and humans, resulted in selection for what we are calling the SELF system, a system that enhances locomotor capacities. The potentially great selective importance of these capacities is apparent from Cant's (1992a) observation that the basic components of reproductive success, such as finding food and mates and

avoiding predators, depend directly on the effectiveness with which an animal negotiates its habitat. Thus, one may reason that as body mass evolved in the great ape/human lineage past some deformation-related limit, and degree of arboreality remained constant, selection would have favored those individuals that could deploy effective new solutions to these problems. The SELF system as we envision it integrates explicit representation of the body, with systems for planning and executing locomotor actions in a highly deformable habitat in which supports used by the animal change their locations not only relative to the animal as it moves, which is true for all moving animals, but in relation to each other due to the loads imposed by the animal itself.

Povinelli and Cant (1995) proposed that one of the principal solutions to the problems described above was the increasing dependence upon a particular mode of locomotion called ‘orthograde clambering.’ However, it now seems clear that emphasizing a particular *mode* of locomotion may have diverted attention from the key distinction (admittedly, more difficult to quantify) in the arboreal locomotion of orangutans – a distinction involving a unique *process* of locomotion through highly compliant habitat structures – and caused us to focus on a behavior (clambering) that is too broadly defined to be useful in this context. Povinelli and Cant proposed that this organismal-ecological interface entailed the co-evolution of a more integrated, explicit representation of the body, along with attendant systems for planning and executing these actions in an arboreal environment: what we have now labeled the SELF system.

It is crucial to note our belief that the problems solved by the SELF system are rarely, if ever, encountered by certain smaller-bodied arboreal primates who live in the same habitat as Sumatran orangutans. Consider long-tailed macaques. Their body mass (3.5

to 5.5 kg) is generally too small to generate difficult gaps, and thus for them the canopy functions as a more or less continuous substrate. In those cases where natural gaps are encountered, these smaller-bodied primates can simply leap across them – for scaling reasons, an option not available to 40-80 kg orangutans! Thus, for long-tailed macaques, over 90% of their daily locomotion can be described by highly stereotyped modes of locomotion (walking, running, leaping, etc.; see Cant, 1988). An intermediate, and therefore interesting case, is the siamang, which may weigh as much as 11 kg. Even this body mass would appear to be large enough to make travel along the top of branches less stable, as the siamang's primary mode of locomotion, brachiation, is suspension below branches. However, siamang body mass is apparently not so large as to require the unique process of locomotion practiced by orangutans as they travel through a network of arboreal structures that severely deform under the loads created by their body mass. Siamangs typically cross large gaps in the travel path by leaping on a downward trajectory or dropping (Fleagle, 1976). Furthermore, like long-tailed macaques and other primates, a high proportion of siamang locomotion can be described by stereotyped modes of locomotion. Thus, in contrast to orangutans, other arboreal primates inhabiting the same habitat have apparently not crossed a body mass threshold (the value of which is presently unknown) where deformation of habitat structure becomes so severe that a more explicit body-image becomes necessary to keep track of the body's moment-to-moment effect on the surrounding environment.

Although such problem-solving activities of orangutans during locomotion have been qualitatively described elsewhere (Chevalier-Skolnikoff, Galdikas, & Skolnikoff, 1982; Povinelli & Cant, 1995; Cant, 1992b), what is needed now is the development of

methods that can produce *quantifiable* estimates of the difference in the complexity of habitat deformation and the orangutan's response to it during bouts of locomotion through highly compliant portions of the arboreal habitat, on the one hand, and locomotion in other contexts where supports are relatively rigid and deformation is limited, on the other. A critical component of such research efforts will be the development of reliable methods for describing, and then comparing, the maximum complexity of habitat deformation created by the very large bodied orangutans, to that created by considerably smaller-bodied arboreal lesser apes and New World monkeys (such as spider monkeys and woolly monkeys) whose body mass (one-quarter that of female orangutans) is still considerable enough to create a non-trivial degree of habitat deformation. Inter-specific comparisons of this kind should allow us to identify the unique "signatures" of habitat deformation generated by very large-bodied apes, as well as their behavioral responses to such deformation, with the ultimate aim of more clearly specifying the unique challenges faced by these animals.

Arboreal gap-crossing and life history parameters in comparative perspective

Focusing just on the four species of extant great apes (chimpanzees, bonobos, orangutans, and gorillas), our model posits a relationship between arboreality, body mass, and body image. (Humans, of course, are a special case that we shall examine in a moment.) Table 1 organizes what is currently known about degree of arboreality, body mass, and mirror self-recognition in the extant great apes. Using the last common ancestor of the great ape/human group as a reference, orangutans appear to have become quite specialized in their behavioral responses to the deformation caused by their body mass while moving through the canopy, gorillas have moved in the opposite direction,

essentially becoming re-terrestrialized, with chimpanzees and bonobos somewhere intermediate.

The most intriguing aspect of the data summarized in Table 1 concerns gorillas. Although there are individual differences in mirror self-recognition among chimpanzees and orangutans⁵ (see e.g. Povinelli et al., 1993), at least three well-controlled studies with lowland gorillas have failed to produce even a single animal that has exhibited compelling evidence of self-recognition (see earlier discussion). Not surprisingly, the gorilla's re-adaptation to a terrestrial way of life appears to have had consequences for certain aspects of its life history. Compared to orangutans, gorillas exhibit an accelerated pattern of development in virtually all areas: they locomote independently at a younger age, they are weaned sooner, and exhibit earlier menarche and age at first birth. Although the data are not excellent, chimpanzees and bonobos again appear to be somewhat intermediate (see Povinelli & Cant, 1995). Finally, and perhaps more importantly, gorillas appear to develop certain aspects of physical maturity not just absolutely faster, but also when compared to

⁵ Although there would appear to be reliable individual differences in the capacity for mirror self-recognition among chimpanzees (see Swartz & Evans, 1991; Povinelli et al., 1993; deVeer et al., 2002), several researchers have construed the existing data in a highly questionable manner. For example, at least 3 separate reviews of the self-recognition literature have cited the most definitive population-level study to date, Povinelli et al. (1993), as having produced evidence that only 30/92 (33%) of chimpanzees exhibited behavioral evidence of self-recognition (SR+), and/or only 13/42 (31%) passed the mark test (see Heyes, 1994; Westergaard & Hopkins, 1994; Swartz et al., 1999). These numbers were obtained by collapsing across all age groups that Povinelli et al. tested: a grossly flawed procedure given the strong ontogenetic trends that were reported, and highlighted, by the original authors. For example, most of the chimpanzees tested by Povinelli et al. were under 5 years of age, and the data set clearly reveals that the onset of the capacity peaks at around 8-16 years of age (at which 70-80% of all animals, based on stringent behavioral criteria, exhibited the capacity). Furthermore, the mark tests *specifically targeted* an equal sample size of subjects who were classified as SR+ or SR-: they were not selected at random as implied by the reviews cited above. To be clear, the analytical technique used by these reviews is analogous to combining data from a large number of 10-month-old human infants with data from a handful 5-year-old children and adults, in order to obtain an estimate for the percentage of humans that are capable recognizing themselves in mirrors.

certain aspects of intellectual development (e.g., Redshaw, 1978; Chevalier-Skolnikoff, 1983; Spinozzi & Natale, 1989; Antinucci, 1990; Parker 1999).

One possible conclusion from these data is that as the gorilla lineage was evolving towards a more terrestrial way of life, they no longer needed the SELF system (which evolved to sub-serve behavioral solution to the habitat deformation occurring during arboreal locomotion), and hence were free to ‘trade off’ this system in favor of more rapid physical maturation. Indeed, data which suggest that gorillas exhibit accelerated physical maturation relative to intellectual development (see above), provide some circumstantial evidence in support of this view (see discussion by Povinelli, 1994). If these data are corroborated, substantial weight would be added to the hypothesis that the basic genetic instructions for those systems are still present in modern gorillas, but are turned off due to shifts in the rate and timing of development (for empirical details which support this possibility, see Povinelli, 1994). However, we should quickly add that it remains unclear what aspects of the SELF system, precisely, might have been traded off during the evolution of gorilla development. It is possible that gorillas possess a body image⁶ indistinguishable from primates outside the great ape/human group. However, it is also possible that they retain a more integrated body image than other primates, but one that differs in substantial enough ways from the ancestral SELF system to preclude the establishment of an equivalence relation between their body and a contingent mirror image of themselves (see above). In other words, only certain developmental pathways relevant to the SELF system may have been turned off during the course of the evolution of the gorilla

⁶ Given that it is not clear what aspects of the SELF system have been modified, it is unclear whether the term ‘body image’ or ‘body schema’ is most appropriate here. See Footnote 1.

lineage, and thus these animals may still retain a considerably more developed body image than other primates.

Some researchers have pointed out that the fact that humans are even more re-adapted to a terrestrial way of life than are gorillas could represent a stumbling block for the clambering theory (e.g., Gallup, 1998). As explained above, however, terrestriality is relevant only insofar as it is a marker of selection for more rapid physical maturation relative to intellectual development – that is, to the extent that it suggests that certain later-emerging systems may have been turned off due to changes in the rate and timing of development of other systems. Clearly, this is not true in the human case. In fact, it seems obvious that selective forces that operated during human evolution pushed our species in the opposite direction, developmentally speaking, from gorillas. Rather than accelerating physical development, humans evolved an extended period of physical immaturity *and* pushed aspects of general intellectual development considerably later, with all key life history parameters delayed relative to the great apes. To provide a concrete example, humans exhibit independent locomotion at a much later stage of cognitive development than do any of the great apes (e.g., Antinucci, 1990). Indeed, if anything, the overall pattern of development in humans suggests an extended period for the elaboration of the self-concept (along many dimensions), not a truncation of this period.

Other “fingerprints” of SELF

Although the nature of the SELF system is at present only weakly specified, several key aspects of Povinelli and Cant’s (1995) theory can now be highlighted.

First, the hypothesis posits that the great apes and humans possess a body image that is, in some contexts, available as a concept, or object of knowledge in its own right.

Whereas many species have proprioceptive and kinesthetic systems which have evolved to regulate complex patterns of movement through space, it may be the case that only the great apes and humans have elevated knowledge of the body as an object of knowledge in itself.

Second, it is possible that the SELF is the fundamental platform of the more elaborated dimensions of the self which exist in humans – dimensions which may or may not exist in great apes, and other species. If so, even now it could still be the body, not the mind, which is first and foremost available to the developing human infant, and thus this dimension of the self may retain a kind of phenomenological primacy as other, psychological aspects of the self begin to emerge (see Povinelli, 2001).

Third, if the SELF evolved as an adaptation for coping with the problem that increasing body mass generated for arboreal locomotion in the last common ancestor of the great apes and humans, then its detection millions of years later by Gallup (1970) and his mirror test was curiously serendipitous. After all, if our model has merit, then in attempting to discover whether chimpanzees might be able to recognize themselves in mirrors, Gallup would have inadvertently uncovered a system honed by natural selection millions of years earlier for a completely unrelated function; it just so happened that some of the properties of mirrors happen to engage the SELF system! On this view, we should expect that other abilities may be dramatically facilitated by, or in some cases, even allowed for, by the SELF system. Many authors, for example have discussed the connection between the representation of one's body and imitation (Baldwin, 1901; Merleau-Ponty, 1962; Mitchell, 1993; Meltzoff, 1990). Although many acts of imitation may be possible without the presence of the kind of body-image we are describing, it seems increasingly clear that

reproduction of another's actions (broadly construed) can be achieved through multiple routes. Thus, it is possible that the emergence of the SELF system, by adding a level of explicitness to the self, incidentally augmented the tendencies for orangutans and chimpanzees to reproduce the actions of others. Another example may be tool-use. Although many species use, and even fashion tools, in certain species the presence of the SELF system may facilitate the discovery and deployment of tools as objects separate and explicitly distinct from the thing that deploys them (for example, 'my hand') (see Povinelli, 2000, pp. 328-337). In short, the SELF system, which initially evolved as an adaptation to subserve effective locomotion in primates with very large body masses, may express itself (imperfectly) in many contexts, only one of which is mirror self-recognition.

Importantly, the flip side of this coin may be true as well. It may be that the surprising within-species individual differences in mirror self-recognition among chimpanzees and orangutans (see above) are both real and a reflection of the fact that the fundamental cognitive system that supports mirror self-recognition, evolved for other purposes, and therefore only imperfectly map on to the mirror test (or any other test not specifically related to the evolutionary context in which it evolved). In short, individual differences in the robustness of the SELF system that have little or no consequence on the ability to negotiate through highly compliant arboreal habitat may have large differences on tests of mirror self-recognition. This fact may also help explain the previously puzzling findings of declines in mirror self-recognition in adulthood in chimpanzees (see Povinelli et al., 1993; de Veer et al., 2002). After all, what is 'declining' might either be the robustness of the system (not typically used in captivity) or incidental factors which allow for self-recognition, but are not essential to the kinesthetic self needed for effective arboreal

locomotion. In addition, this helps to flesh out our earlier explanation of why the absence of behavioral patterns indicative of self-recognition in gorillas may not be so surprising.

It should be emphasized that at present our model is merely a framework pointing to a particular ecological problem (travel through extremely compliant, arboreal habitats by very large-bodied apes) that may have driven a more explicit representation of the body and a suite of motor planning systems designed to sub-serve effective locomotion. It does not specify (a) the scope of this SELF system, or (b) the extent of the evolutionary ‘re-description’ (*sensu* Karmiloff-Smith, 1992) that the proprioceptive and/or kinesthetic systems have undergone. Furthermore, it does not specifically indicate which motor planning systems were most affected and/or elaborated by the evolution of the SELF system. In short, at present, the hypothesis fails to specify a causal account of what specific cognitive systems are necessary to support the process of locomotion we have identified as crucial to our model. Because of this present level of ambiguity in the theory, and the theoretical difficulties in reducing that ambiguity, for the time being we advocate a broad-based approach to understanding how the evolutionary forces which sculpted the unique process of arboreal locomotion exhibited by modern orangutans might have affected the representation and use of the body image, broadly construed.

Novel Tests of the SELF Hypothesis

If, as we have been speculating, the mirror test is just one (albeit straight-forward) way of tapping into the SELF system, then a particularly profitable method of testing the clambering hypothesis might be to determine if the great apes differ in as-of-yet undefined ways from other primates in areas related to the use of and/or reasoning about the body-image. In what follows, we focus on one approach along these lines that we have pursued.

First, we describe how the SELF system may have endowed organisms with a tool-using tendency that, until now, has not been widely recognized. Second, we describe a simple experiment that we conducted to determine if chimpanzees, at least, possess this ability.

Tool-use, tool-discovery, and the SELF

Previously, we had speculated that if chimpanzees and orangutans possess a SELF system, this could explain why they are such expert tool-users: they may possess a more explicit representation of their bodies and their actions, and hence they may more clearly consider self-object relations (see Povinelli, 2000, pp. 228-337). Tool-use exists in a wide range of animal species (see Beck, 1980, for a broad overview), and we are certainly not suggesting that a SELF system is required to produce such behaviors. Rather, the hypothesis is simply that the more explicitly the distinction between self and object can be represented, the more rapidly tool-use will emerge. The sheer diversity of the tool-kits of chimpanzees in the wild, and the remarkable tool-using and tool-making capacities of chimpanzees and orangutans in captivity, suggest that a more explicit representation of the self's body and actions may dramatically speed up the discovery and use of tools.⁷

The prototypical case of tool use involves the animal using a tool as an extension of the hand in order to rake an out-of-reach object close enough that it can be grasped with the

⁷ A contrast between orangutans and gorillas is of interest here. Orangutans do exhibit tool-making and tool-use in the wild (e.g., van Schaik, Fox, & Sitompul, 1996), but it is certainly not as extensive as chimpanzee tool-making and tool-use. If the definition of tool is expanded to include the remarkable use the deformation of smaller tree trunks to assist in the translocation of their body through space ('tree-swaying'), then the amount of orangutan tool-using behavior might easily exceed that of chimpanzees. Indeed, in captivity, orangutans seem to be remarkably pre-adapted to tool-making and tool-use (e.g., Lethmate, 1982). In contrast, gorillas almost never use tools in the wild (even under the broadest definitions available), and although they certainly can and do learn to use tools in captivity, the extent of such behavior does not appear to be as elaborated as in orangutans and chimpanzees (see Fontanie, Moisson, & Wicklings, 1995; Boysen et al., 1999). This later claim, however, is largely based on subjective impressions, rather than quantitative data that might be obtained from an extensive survey of zoological collections.

hand. For the purposes of the present research, however, we were interested in the opposite case: where an object of interest is within reach, but the animal does not wish to directly touch it because it is alarming in some way. Would the chimpanzees spontaneously appreciate that a tool could be used to move the alarming object out of the way, or to gather information about it, so that they did not have to touch it directly? It occurred to us that if chimpanzees and orangutans really do possess a more explicit representation of their bodies (by virtue of their possession of the SELF system), then they might exhibit such behavior spontaneously (see Povinelli, 2000, p. 335). After all, if these species represent their bodies more explicitly, then as they act upon an object with a tool, they may have at their disposal separately accessible representations of (a) their hand acting on the tool, and (b) the tool acting on the object.⁸

An experimental test

To explore this idea, we tested seven captive adult chimpanzees (Barth & Povinelli, manuscript in preparation), all of whom have had an exceptional amount of experience with using tools in a wide variety of tasks (see Povinelli, 2000, for details on their rearing and testing history). The subjects were tested behind a plexiglas partition that contained three openings through which the subjects could freely respond (a procedure with which they were intimately familiar). When the chimpanzees entered, they always found three sticks on

⁸ The use of such explicit representations could be contrasted with, for example, studies with monkeys that have shown that when a monkey uses a tool to retrieve distant objects the neuronal schema that codes for the hand extends to include the space around the distant object (Iriki, Tanaka, & Iwamura, 1996). Across trials, objects that were represented as being in the extra-personal space, become coded as near objects, if a physical extension of the body (a tool) is used. Although this coding of far objects as near objects in bimodal neurons during tool-use has also been found in humans (Farné & Làdavas, 2000; Berti & Frassinetti, 2000), we posit an additional representation in humans and the great apes which allows for the representation of ‘my hand’ to mediate these lower-level representations.

the floor of the test unit, always in the same position. Most of the trials were *standard tool-using trials*, where a piece of food was sitting on the other side of the partition, out of the chimpanzees' immediate reach. On these trials, the chimpanzees easily demonstrated an understanding that they could use one of the sticks to rake in the reward (a hardly surprising feat, given their previous experience; see Povinelli, 2000).

The key findings, however, came from the *test trials* which were administered at certain intervals between the standard tool-using trials. On these trials, a large box with the open side facing the subject was present on the floor directly in front of the plexiglas partition, and was always positioned the same distance from the subject. A highly desirable food reward (either an apple or a banana) and/or an alarming object were then positioned just inside the box so that they were clearly visible to the chimpanzee and easily within his/her reach. The alarming objects included furry toy animals, rubber snakes, and spiders (the alarming potential of the objects was tested informally on a different group of chimpanzees prior to the beginning of the experiment).

A total of six different kinds of test trials were used (with each animal receiving four trials of each kind). Four of these six conditions consisted of the trials just described: (1) food-only, (2) alarming-object-only, (3) food-beside-alarming-object, and (4) food-behind-alarming-object. Two other conditions were also used that were identical to the food-only and alarming-object-only conditions except that the entire box was covered by a cloth so that the subject did not know what was inside unless he or she removed the cloth: (5) covered/food-only and (6) covered/alarming-object-only. As before, the sticks were present, available to the subjects if they chose to use them. Thus, the chimpanzees were free to make contact with the food and/or the object, either by using their hands, using one of

the tools as a mediator, or to ignore the situation altogether. The significant aspect of this design was that on all test trials, the food and the alarming objects were always the same distance from, and easily within reach of, the individual chimpanzees.

We reasoned that in the food-beside-alarming-object and food-behind-alarming-object conditions, an organism with a SELF system would be highly likely to make the inference that the tool could be used to push the alarming object out of the way, and thus avoid having to make direct bodily contact with the object as they reached for the food. Similar logic applied to the two conditions in which the box was covered, and the chimpanzees were therefore ignorant of what was inside: they ought to use the tool to remove the cloth before reaching with their hands. Finally, on the alarming-object-only trials we reasoned that in the absence of food, the subjects would be interested in exploring the alarming object, but that they ought to use the tool, not their hands, to do so. All of these conditions could be contrasted with the food-only condition, in which we expected that the subjects would simply reach directly with their hand to take the food. On the other hand, if the subjects simply conceived the tool as an extension of their arm, they would be expected to be quite hesitant to contact the alarming object, even with the tool. Our primary measure was the number of bouts that the subjects used their hands versus the tools across the six conditions.

The two conditions in which the contents of the box were covered turned out to be the most pivotal. Three of our seven apes consistently used one of the provided tools to uncover the concealed box before they reached with their hands in these two conditions (see Figure 6). The remaining four apes either removed the cloth by hand or did not respond at all. The behavior on these ‘covered’ conditions predicted their behavior on the

other conditions. The chimpanzees that uncovered the box by using a tool also used the tool consistently on the conditions in which an alarming object was present, but not on the food-only trials. They used the tool to move the object away from the food (or the food away from the object) and they used the tool to explore the object. They only rarely made contact with the object by using their hands, and if they did, only *after* they first explored it with the tool. Likewise, they only rarely retrieved the food directly without first increasing the distance between food and object by using the tool. In contrast, the four apes that reached to unveil the box with their hands in the covered conditions, also only used the tool randomly with respect to the other conditions, if they used it at all.

Importantly, all of the apes directly retrieved the food from the box by using their hands in the food-only condition. This demonstrates that the three apes who used the tool only when the alarming object was present, and when they did not know what was in the box, clearly distinguished between the conditions and did not simply use the tool for idiosyncratic reasons, such as overestimating the distance between themselves and the box. Rather, they used the tool only on those trials during which their hand would have to touch, or come too close to touching, an alarming object.

Although the results are preliminary, they suggest that at least three of our chimpanzees provided reliable evidence of utilizing an explicit representation of their hand when they used the tool as a mediator between their hand and the object. Not all of our apes did so, however. Indeed, our apes could be classified into two groups, those that did use the tool as a mediator and those that did not. This difference cannot be explained by individual differences in tool-using expertise, as all of the apes were proficient tool-users with an exceptional amount of practice and experience on a wide variety of tasks (see Povinelli,

2000). More directly, in the present study, all of the subjects used the tools to retrieve the food reward easily on the standard tool-using trials (see above). So, why did only about half of them use the tool as a mediator? As noted above, perhaps it is because the SELF system we are probing evolved in a different context, one that only imperfectly maps itself into the present test situation.

Although we have not yet conducted our test with other species – in particular, those that do not exhibit evidence of self-recognition – comparative tests of this sort (especially a direct comparison between great apes and several species of Old and New World monkeys) would be of great interest. At present, we offer these data as a possible illustration of how the SELF system we hypothesize to exist in the great apes and humans- a system which has heretofore been explored only through the mirror test- may express itself in other contexts as well.

Concluding Reflections on SELF

In this essay, we have elaborated upon a hypothesis first put forward by Povinelli and Cant (1995) that the evolutionary origins of the self-concept may be found in a unique set of ecological circumstances faced by the ancestors of the great apes and humans – a set of factors that selected for the development of an explicit representation of the body and an understanding of its ongoing effects on the environment. In doing so, we have not sought to downplay the importance of the myriad, implicit kinesthetic and proprioceptive systems that allow organisms to function in the environments they inhabit. Indeed, a wealth of research in developmental psychology, cognitive neuroscience, and motor planning, has explored the nature of the body image/schema, elucidating the mechanisms that allow

organisms ranging from human infants to bats to fishes to elephants to integrate somatosensory and visual information, and distinguish self from environment.

Nonetheless, it seems likely that a fundamentally new representation of the self – what we have labeled the SELF system – evolved for roughly the reasons outlined almost a decade ago by Povinelli and Cant (1995). But this new, integrated representation of the body may have done more than endow those organisms to exhibit the rather remarkable ability for self-recognition in mirrors. It may have pre-adapted these species for more elaborated forms of tool-use, new ways of relating to the bodily acts of others, and more flexible use of manual-based signals, just to name a few. And, if we are right, this may just be the tip of the iceberg; it may be that when it comes to cascading effects of the evolution of the SELF, there may exist numerous (and as-of-yet unexplored) species differences between the great apes and humans on the one hand, and most other forms of life on the other. A subtle, but distinct thread may thus run through the actions of humans and the other great apes, a kinematic signature of a SELF we share due to our common ancestry.

References

- Anderson, J. R., & Roeder, J.-J. (1989). Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror-image stimulation. *Primates*, *30*, 581-587.
- Anderson, J. R., & Gallup, G. G. (1997). Self-recognition in Saguinus? A critical essay. *Animal Behaviour*, *54*, 1563-1567.
- Anderson, J. R., & Gallup, G. G., Jr. (1999). Self-recognition in nonhuman primates: Past and future challenges. In M. Haug & R. E. Whalen (Eds.), *Animal models of human emotion and cognition* (pp. 175-194). Washington, DC, US: American Psychological Association.
- Antinucci, F. (1990). The comparative study of cognitive ontogeny in four primate species. In S. T. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: comparative developmental perspectives*. New York, NY, US.: Cambridge University Press.
- Asendorpf, J. B., & Baudonniere, P.-M. (1993). Self-awareness and other-awareness: Mirror self-recognition and synchronic imitation among unfamiliar peers. *Developmental Psychology*, *29*, 88-95.
- Barth, J., & Povinelli, D. J. (Manuscript in preparation). An experimental study with captive chimpanzees (*Pan troglodytes*) on the use of a tool as a mediator in a food-object conflict task.
- Beck, B. B. (1980). *Animal Tool Behavior*. New York, NY, US: Garland Publishing, Inc.
- Berlucchi, G., & Aglioti, S. (1997). The body in the brain: neural bases of corporeal awareness. *Trends in Neurosciences*, *20*, 560-564.

- Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience*, *12*, 415-420.
- Bischof-Koehler, D. (1988). On the connection between empathy and the ability to recognize oneself in the mirror. [German]. *Schweizerische Zeitschrift Fuer Psychologie*, *47*, 147-159.
- Boysen, S. T., Kuhlmeier, V. A., Halliday, P., & Halliday, Y. M. (1999). Tool use in captive gorillas. In S. T. Parker & R. W. Mitchell (Eds.), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 179-187). New York, NY, US: Cambridge University Press.
- Brooks-Gunn, J., & Lewis, M. (1984). The development of early visual self-recognition. *Developmental Review*, *4*, 215-239.
- Butterworth, G. (1992). Origins of self-perception in infancy. *Psychological Inquiry*, *3*, 103-111.
- Butterworth, G. (1995). An ecological perspective on the origins of self. In J. L. Bermudez & A. J. Marcel (Eds.), *The body and the self* (pp. 87-105). Cambridge, MA, US: The MIT Press.
- Cant, J. G. (1987). Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). *American Journal of Primatology*, *12*, 71-90.
- Cant, J. G. H. (1988). Positional behavior of long-tailed macaques in northern Sumatra. *American Journal of Physical Anthropology*, *76*, 29-37.
- Cant, J. G. H. (1992a). Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *American Journal of Physical Anthropology*, *88*, 273-283.

- Cant, J. G. H. (1992b). Positional behavior of arboreal primates and habitat compliance. In B. Thierry, J. R. Anderson, J. J. Roeder & N. Herrenschildt (Eds.), *Current Primatology. Volume 1. Ecology and Evolution* (pp. 187-193). Strasbourg: Université Louis Pasteur.
- Cartmill, M. (1974). Rethinking primate origins. *Science*, *184*, 436-443.
- Chevalier-Skolnikoff, S. (1983). Sensorimotor development in orang-utans and other primates. *Journal of Human Evolution*, *12*, 545-561.
- Davis, L. H. (1989). Self-consciousness in chimps and pigeons. *Philosophical Psychology*, *2*, 249-259.
- de Veer, M., van der Bos, Theall, L. A., Gallup, G.G., Jr., & Povinelli (2002). An eight-year longitudinal study of self-recognition in chimpanzees. *Neuropsychologia*, *1493*, 1-6.
- Eddy, T. J., Gallup, G. G., Jr., & Povinelli, D. J. (1996). Age differences in the ability of chimpanzees to distinguish mirror-images of self from video images of others. *Journal of Comparative Psychology*, *110*, 38-44.
- Farne, A., & Ladavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, *11*, 1645-1649.
- Fivush, R. (2001). Owning experience: Developing subjective perspective in autobiographical narratives. In C. Moore & K. Lemmon (Eds.), *The self in time: Developmental perspectives* (pp. 35-52). Mahwah, NJ, US: Lawrence Erlbaum Associates, Inc., Publishers.
- Fontaine, B., Moisson, P. Y., & Wickings, E. J. (1995). Observations of spontaneous tool making and tool use in a captive group of western lowland gorillas (*Gorilla gorilla*

- gorilla). *Folia Primatologica*, 65, 219-223.
- Gallagher, S. (1986). Body image and body schema: A conceptual clarification. *Journal of Mind & Behavior*, 7, 541-554.
- Gallup, G. G., Jr. (1968). Mirror-image stimulation. *Psychological Bulletin*, 70, 782-793.
- Gallup, G. G. (1970). Chimpanzees: Self-recognition. *Science*, 167, 86-87.
- Gallup, G. G. (1977). Self recognition in primates: A comparative approach to the bidirectional properties of consciousness. *American Psychologist*, 32, 329-338.
- Gallup, G. G., Wallnau, L. B., & Suarez, S. D. (1980). Failure to find self-recognition in mother-infant and infant-infant rhesus monkey pairs. *Folia Primatologica*, 33, 210-219.
- Gallup, G. G. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology*, 2, 237-248.
- Gallup, G. G. (1985). Do minds exist in species other than our own? *Neuroscience and Biobehavioral Reviews*, 9, 631-641.
- Gallup, G. G., Jr. (1994). Self-recognition: Research strategies and experimental design. In S. T. Parker & R. W. Mitchell (Eds.), *Self awareness in animals and humans: Developmental perspectives* (pp. 35-50). New York, NY, USA: Cambridge University Press.
- Gallup, G. G., Jr. (1998). Self-awareness and the evolution of social intelligence. *Behavioural Processes*, 42, 239-247.
- Hauser, M. D., Kralik, J., Botto-Mahan, C., Garrett, M., & Oser, M. (1995). Self-recognition in primates: Phylogeny and the salience of species-typical features. *Proceedings of the National Academy of Science*, 92, 10811-10814.

- Hauser, M. D., Miller, C. T., Liu, K., & Gubta, R. (2001). Cotton-top tamarins (*Saguinus oedipus*) fail to show mirror-guided self-exploration. *American Journal of Primatology*, *53*, 131-137.
- Head, H. (1920). *Studies in Neurology* (Vol. 2). London: Oxford University Press.
- Heyes, C. M. (1994). Reflections on self-recognition in primates. *Animal Behaviour*, *47*, 909-919.
- Heyes, C. M. (1995). Self-recognition in primates: Further reflections create a hall of mirrors. *Animal Behaviour*, *50*, 1533-1542.
- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral & Brain Sciences*, *21*, 101-134.
- Howe, M. L., & Courage, M. L. (1993). On resolving the enigma of infantile amnesia. *Psychological Bulletin*, *113*, 305-326.
- Howe, M. L., & Courage, M. L. (1997). The emergence and early development of autobiographical memory. *Psychological Review*, *104*, 499-523.
- Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing Points in Ethology* (pp. 303-317). Cambridge, UK.: Cambridge University Press.
- Hyatt, C. W. & Hopkins, W. D. (1994). Self-awareness in bonobos and chimpanzees: A comparative perspective. In S.T. Parker & R. W. Mitchell (Ed.), *Self-awareness in Animals and Humans: Developmental Perspectives*. New York: Cambridge University Press.
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport*, *7*, 2325-2330.

- Johnson, D. B. (1982). Altruistic behavior and the development of the self in infants. *Merrill-Palmer Quarterly*, 28, 379-388.
- Karmiloff-Smith, A. (1992). *Beyond modularity: A developmental perspective on cognitive science*. Cambridge, MA: MIT Press.
- Larson, S. K. (1988). *Individual differences in physiology, behavior, and temperament over the first 15 months of life*. University of Illinois, Urbana-Champaign, US.
- Ledbetter, D. H., & Basen, J. A. (1982). Failure to demonstrate self-recognition in gorillas. *American Journal of Primatology*, 2, 307-310.
- Lethmate, J. (1982). Tool-using skills of orang-utans. *Journal of Human Evolution*, 11, 49-64.
- Lewis, M., Sullivan, M. W., Stanger, C., & Weiss, M. (1989). Self development and self-conscious emotions. *Child Development*, 60, 146-156.
- Loveland, K. A. (1986). Discovering the affordances of a reflecting surface. *Developmental Review*, 6, 1-24.
- Martin, M. G. F. (1995). Bodily awareness: A sense of ownership. In J. L. Bermudez, A. J. Marcel & E. Naomi (Eds.), *The Body and the self*. Cambridge, MA, US: The MIT Press.
- Meltzoff, A. N. (1990). Foundations for developing a concept of self: The role of imitation in relating self to other and the value of social mirroring, social modeling, and self practice in infancy. In D. Cicchetti & M. Beeghly (Eds.), *The self in transition: Infancy to childhood*. (pp. 139-164). Chicago, IL, US: The University of Chicago Press.
- Meltzoff, A. N., & Moore, M. K. (1999). Persons and representation: Why infant imitation

- is important for theories of human development. In J. Nadel & G. Butterworth (Eds.), *Imitation in infancy. Cambridge studies in cognitive perceptual development* (pp. 9-35). New York, NY, US: Cambridge University Press.
- Merleau-Ponty, M. (1962). *Phenomenology of Perception*. London: Routledge and Kegan Paul.
- Mitchell, R. W. (1993). Mental models of mirror-self-recognition: Two theories. *New Ideas in Psychology, 11*, 295-325.
- Nelson, K. (1992). Emergence of autobiographical memory at age 4. *Human Development, 35*, 172-177.
- Parker, S. T. (1999). The life history and development of great apes in a comparative perspective. In S. T. Parker & R. W. Mitchell (Eds.), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 43-69). New York, NY, US: Cambridge University Press.
- Povinelli, D. J. (1989). Failure to find self-recognition in Asian elephants (*Elephas maximus*) in contrast to their use of mirror cues to discover hidden food. *Journal of Comparative Psychology, 103*, 122-131.
- Povinelli, D. J., Rulf, A. B., Landau, K. R., & Bierschwale, D. T. (1993). Self-recognition in chimpanzees (*Pan troglodytes*): Distribution, ontogeny, and patterns of emergence. *Journal of Comparative Psychology, 107*, 347-372.
- Povinelli, D. J. (1994). How to create self-recognizing gorillas (but don't try it on macaques). In S. T. Parker & R. W. Mitchell (Eds.), *Self awareness in animals and humans: Developmental perspectives* (pp. 291-300). New York, NY, USA: Cambridge University Press.

- Povinelli, D. J., & Cant, J.G.H. (1995). Arboreal clambering and the evolution of self-conception. *The Quarterly Review of Biology*, *70*, 393-421.
- Povinelli, D. J. (1995). The unduplicated self. In P. Rochat (Ed.), *The self in infancy: Theory and research. Advances in psychology*, *112* (pp. 161-192). Amsterdam, Netherlands: North-Holland/Elsevier Science Publishers.
- Povinelli, D. J., Landau, K. R., & Perilloux, H. K. (1996). Self-recognition in young children using delayed versus live feedback: Evidence of a developmental asynchrony. *Child Development*, *67*, 1540-1554.
- Povinelli, D. J., Gallup, G. G., Jr., Eddy, T. J., & Bierschwale, D. T. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behaviour*, *53*, 1083-1088.
- Povinelli, D. J., & Simon, B. B. (1998). Young children's understanding of briefly versus extremely delayed images of the self: Emergence of the autobiographical stance. *Developmental Psychology*, *34*, 188-194.
- Povinelli, D. J., Landry, A. M., Theall, L. A., Clark, B. R., & Castille, C. M. (1999). Development of young children's understanding that the recent past is causally bound to the present. *Developmental Psychology*, *35*, 1426-1439.
- Povinelli, D. J. (2000). *Folk Physics for Apes*. New York, NY, US: Oxford University Press.
- Povinelli, D. J. (2001). The self: Elevated in consciousness and extended in time. In C. Moore & K. Lemmon (Eds.), *The self in time: Developmental perspectives* (pp. 75-95). Mahwah, NJ, US: Lawrence Erlbaum Associates.
- Priel, B., & de Schonen, S. (1986). Self-recognition: A study of a population without mirrors. *Journal of Experimental Child Psychology*, *41*, 237-250.

- Redshaw, M. (1978). Cognitive development in human and gorilla infants. *Journal of Human Evolution*, 7, 133-141.
- Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Science*, 98, 5937-5942.
- Robinson, J. A., Connell, S., McKenzie, B. E., & Day, R. H. (1990). Do infants use their own images to locate objects reflected in a mirror? *Child Development*, 61, 1558-1568.
- Shillito, D. J., Gallup, G. G., Jr., & Beck, B. B. (1999). Factors affecting mirror behaviour in western lowland gorillas, *Gorilla gorilla*. *Animal Behaviour*, 57, 999-1004.
- Spinozzi, G., & Natale, F. (1989). Early sensorimotor development in Gorilla. In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates*. Hillsdale, NJ, US.: Lawrence Erlbaum Associates.
- Suarez, S. D., & Gallup, G. G. (1981). Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution*, 10, 175-188.
- Suarez, S. D., & Gallup, G. G., Jr. (1986) Social responding to mirrors in rhesus macaques (*Macaca mulatta*): Effects of changing mirror location. *American Journal of Primatology*, 11, 239-244.
- Sugardjito, J., & Van Hooff, J. A. (1986). Age-sex class differences in the positional behaviour of the Sumatran orang-utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. *Folia Primatologica*, 47, 14-25.
- Swartz, K. B., & Evans, S. (1991). Not all chimpanzees (*Pan troglodytes*) show self-recognition. *Primates*, 32, 483-496.

- Swartz, K. B., Sarauw, D., & Evans, S. (1999). Comparative aspects of mirror self-recognition in great apes. In S. T. Parker & R. W. Mitchell (Eds.), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 283-411). New York, NY, US: Cambridge University Press.
- van Schaik, C. P., Fox, E. A., & Sitompul, A. F. (1996). Manufacture and use of tools in wild orangutans. *Naturwissenschaften*, 83, 186-188.
- Walraven, V., Elsacker, L., & Verheyen, R. (1995). Reactions of a group of pygmy chimpanzees (*Pan paniscus*) to their mirror-images: Evidence of self-recognition. *Primates*, 36, 145-150.
- Welch-Ross, M. K. (1999). Preschoolers' understanding of mind: Implications for suggestibility. *Cognitive Development*, 14, 101-131.
- Westergaard, G. C., & Hopkins, W. D. (1994). Theories of mind and self-recognition. *American Psychologist*, 49, 761.

Table 1

Mirror Self-Recognition Status, Body Mass, and Complexity of Arboreal Locomotion in the Extant Great Apes

Species	Mirror Self-Recognition Status	Body Mass Rank ^a (kg, male/female)	Complexity of Arboreal Travel ^b
Orangutan	+	2 (78/35)	1
Bonobo	+	4 (45/33)	2
Chimpanzee	+	3 (50/41)	3
Gorilla	-	1 (169/80)	4 (terrestrial)

Notes. ^aBody mass in kg from Fleagle (1999, Table 7.2, body mass among sub-species was averaged). ^bSpecies ranks for arboreal travel are derived from estimates of time spent in complex positional behavior while crossing from one tree to the next.

Figure Captions

Figure 1. A 5½-year-old chimpanzee (a) exhibiting exaggerated facial expressions and (b-d) otherwise invisible parts of her body while observing herself in a mirror.

Figure 2. Method and results of mark test: (a) while under anesthesia, regions of the subject's face are targeted to be marked with a red dye (shaded areas) and contralateral facial regions (unshaded areas) are targeted as control areas, and upon full recovery (b) subjects is exposed to a covered mirror for 30 minutes, followed immediately by 30 minutes of exposure to a mirror. Note that in (b) touches to the facial regions are selective to the marked areas, coincident with the uncovering of the mirror, and decline after the subject discovers that the marks are inconsequential.

Figure 3. Phylogeny of the great apes and humans showing lesser apes (gibbons and siamangs) and old world monkeys as outgroups. The split between the orangutans and the African apes and humans occurred approximately 15-20 million years ago.

Figure 4. Results of a test to determine if 3-, 4- and 5-year-olds can distinguish between the relevance of videotape showing a sticker having been placed on their heads 7 days earlier (extreme delay) versus 3 minutes earlier (brief delay). As shown here, 4- and 5-year-olds appreciate that only the briefly delayed images are causally relevant to their current appearance. See text for details.

Figure 5. An adult female orangutan crossing a gap between two trees by clambering. Note the infant/juvenile that she is carrying across the gap.

Figure 6. Covered box condition: A chimpanzee subject (a) encounters a covered box and (b-d) spontaneously uses a provided stick to uncover it in order to explore its contents.