

18 How to create self-recognizing gorillas (but don't try it on macaques)

Daniel J. Povinelli

Several years ago, I used the phrase "the anomalous gorillas" while reviewing the nonhuman primate self-recognition literature (Povinelli, 1987, p. 496). At that time, there had been a number of careful, unsuccessful attempts to produce a convincing demonstration of self-recognition in this species (Ledbetter & Basen 1982; Lethmate, cited in Gallup, 1982; Suarez & Gallup, 1981). However, there was one gorilla (Koko) who, based upon uncontrolled (at the time) observations, appeared to show clear signs of self-recognition. The descriptions of Koko's behaviors offered by Patterson (1984) were compelling and comparable to that obtained by Gallup and his colleagues, as well as by other independent researchers working under more controlled conditions with chimpanzees (Calhoun & Thompson, 1988; Gallup, 1970; Gallup, McClure, Hill, & Bundy, 1971; Lethmate & Dücker, 1973; Suarez & Gallup, 1981). Despite this rather remarkable behavior on the part of one member of the species, gorillas as a whole appeared to fall into a different category than chimpanzees, orangutans, and humans with regard to self-recognition. This seemed difficult to reconcile with the evolutionary relatedness of the species within the great ape-human clade; hence my invocation of the phrase "the anomalous gorillas" (Povinelli, 1987).

Several potential explanations for why most gorillas did not appear like chimpanzees on mirror self-recognition tasks suggested themselves, ranging from the hypothesis that they are differentially sensitive to the effects of being reared in captivity, to the possibility that they are simply not motivated to solve the learning problem imposed by the introduction of mirrors (Povinelli, 1987). I also addressed the possibility that gorillas have undergone a character state reversal in the underlying psychological capacity necessary for self-recognition, but I dismissed it on the grounds that was "extremely difficult to envision an organism evolving so unique a mental faculty [as self-awareness] and then losing it through the forces of evolution" (p. 499). Furthermore, I argued that such an explanation was "*ad hoc* and inconsistent with much of what we know about gorilla behavior" (p. 499). In retrospect, it is unclear to what data I was referring; at the time no such data existed for gorillas, and even today no one has yet attempted to provide an experimental demonstration

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of mental state attribution in gorillas. Thus, I am left in the embarrassing position of admitting that I discounted the possibility that gorillas had secondarily lost the capacity for self-recognition on the basis of the assumption that complex mental characteristics should be perfectly correlated with phylogeny. In other words, I viewed complex psychological characteristics as somehow fundamentally different than complex morphological characteristics. However, after exposing a captive group of socially housed gorillas to a large mirror for nearly 4 years now without any evidence of self-recognition (Shumaker & Povinelli, unpublished observations), I appear to have undergone a character state reversal of sorts myself. Upon rethinking the issue, I now believe that the gorillas only seemed anomalous because I allowed certain preconceptions to guide my interpretation of the data.

Self-recognition and gorillas

I believe that the best available interpretation of the status of self-recognition in gorillas is that the ontogeny of most gorillas does not include the construction of the cognitive structures that ultimately support self-exploratory behaviors in front of mirrors. However, although most gorillas tested to date for self-recognition have not shown compelling evidence (Ledbetter & Basen, 1982; Parker, 1990; Shumaker & Povinelli, unpublished observations; Suarez & Gallup, 1981), one home-reared gorilla has shown the full suite of behavioral indices of mirror self-recognition (Patterson, 1984). Some may feel that this description does not do justice to the current state of affairs for self-recognition research in gorillas, citing either facial movements or isolated reports of what appear to be self-directed responses on the part of one gorilla or another (Parker, 1990, 1991; Patterson & Cohn, *SAAH17*). However, in our laboratory, as part of a long-term study of the development of self-recognition in chimpanzees, my colleagues and I have thus far collected extensive systematic observations of 105 mature and immature chimpanzees (Povinelli, Rulf, Landau, & Bierschwale, in press). The chimpanzees that do not display compelling evidence of self-recognition do occasionally show instances of what could arguably be called contingent facial or bodily movements, face making at the mirror, or other instances of self-directed behaviors while the subjects are near the mirror, but not looking into it. But these ambiguous behaviors are not correlated with compelling bouts of contingent facial and body movements or self-exploratory movements, nor do they predict group differences in success of Gallup's mark test. Thus, in no way can they be used as unique evidence of self-recognition.

In clear contrast, subjects described as capable of self-recognition typically show clear, sustained, and unambiguous instances of self-exploration while carefully monitoring their reflections, and this predicts dramatically higher levels of contingent body and facial movements than subjects not so classified. In addition, this classification scheme accurately predicts differences between the groups in terms of their ability to pass controlled mark tests (see

Povinelli et al., in press). We conclude that ambiguous instances of self-directed behaviors should not be used as evidence for self-recognition.

Thus, in direct contrast to my earlier, subjective impressions, I now believe that it is reasonable to predict that only *abnormally* reared gorillas, such as Koko, will ever show convincing signs of self-recognition. In this chapter, I outline my reasons for making this prediction in the form of a hypothesis about the relationship between heterochronic shifts in development and psychological evolution.

Reappearance of ancestral traits

A variety of lines of evidence strongly suggest that the great apes and humans all descended from a common ancestor living in the Miocene (Figure 18.1). Furthermore, since the 1960s most researchers in the field have been convinced that chimpanzees, gorillas, and humans form a monophyletic clade, with orangutans representing the nearest living outgroup (Andrews & Martin, 1987; Goodman, 1962; Marks, 1988). Nonetheless, orangutans show obvious evidence of self-recognition, whereas to date there is convincing evidence for only one gorilla. It is precisely this state of affairs that has made the failure to find self-recognition in gorillas so troublesome to many comparative psychologists. My interpretation of this situation, on the basis of cladistic parsimony, is that the trait of self-recognition was present in the population of the common ancestors of the entire great ape-human clade (see Figure 18.1). If the failure to find self-recognition in gorillas is reliable, then the most parsimonious interpretation is that the species has undergone a secondary loss of the capacity (see Gallup, 1985; Povinelli, 1987). Although I believe this to be the case, I also believe that a much richer understanding of this issue can be obtained by considering the effect of environmental perturbations upon early development.

The reappearance of ancestral characteristics within an individual following experimental interventions during ontogeny are well known to embryologists and developmental biologists in general (Buss, 1987, pp. 112–115; see Frazzetta, 1975). Hampé (1960), for instance, in a widely cited study, demonstrated that by allowing the fibula of chicken embryos to touch the metatarsal bones during development, a series of cascading changes occurred that resulted in the development of the ancestral condition found in *Archaeopteryx*, the first bird (see Figure 18.2). Alberch, Gould, Oster, and Wake (1979) have commented on Hampé's experiments, noting that "it is probable that the genetic capacity for producing these ancestral traits was never lost during more than 200 million years of avian evolution, but merely 'turned off' by failure of the inducing fibula to establish contact with the metatarsals" (p. 311). Numerous other examples are available that emphasize the same point: Perturbations in development can result in the secondary appearance of ancestral traits not typically found in descendant species (Kollar, 1972; Raikow, 1975; Raup & Kaufman, 1983). Perhaps one of the most dramatic instances has come from

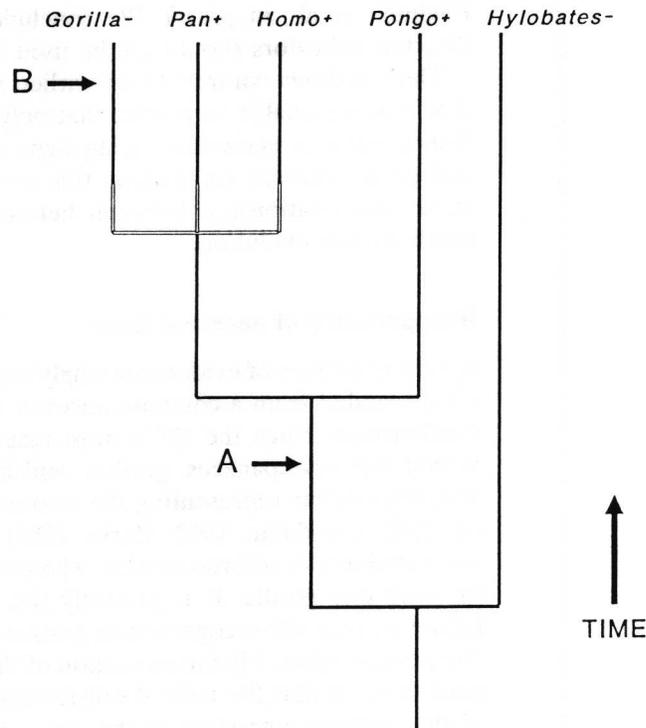


Figure 18.1. Evolutionary relationships of the living apes and humans and the distribution of self-recognition (indicated as + or -). The most parsimonious explanation is obtained by assuming that the underlying capacity for self-recognition evolved once in the ancestor of the great ape grouping (event *A*) and that it has been secondarily lost during the 5–10 million years of independent evolution in the gorilla lineage (event *B*). Note that the African ape–human clade is represented as an uncertain trichotomy due to the continuing controversy that now surrounds the exact relationships of these species (see Marks, 1991).

an experiment by Kollar and Fisher (1980), who demonstrated that the jaw epithelium of chicken embryos will develop teeth when simply placed on the jaw mesoderm of mice. This represents the retention of a capacity to respond to developmental signals that have not been in operation for at least 80 million years. Alberch and his colleagues note, “Latent capacities for the generation of ancestral structures probably exist in the genomes of all specialized animals” (p. 311).

But what of the loss of such characteristics in the first place? There is ample evidence to suggest that many (if not most) evolutionary innovations (losses or additions of particular traits) are achieved through *heterochrony*, changes in the timing and onset of developmental pathways of specific cell lineages (Buss, 1987; Gould, 1977; Raup & Kaufman, 1983). Thus, natural selection may often favor specific variants that are ultimately produced through heterochronic shifts in development. There are several important implications

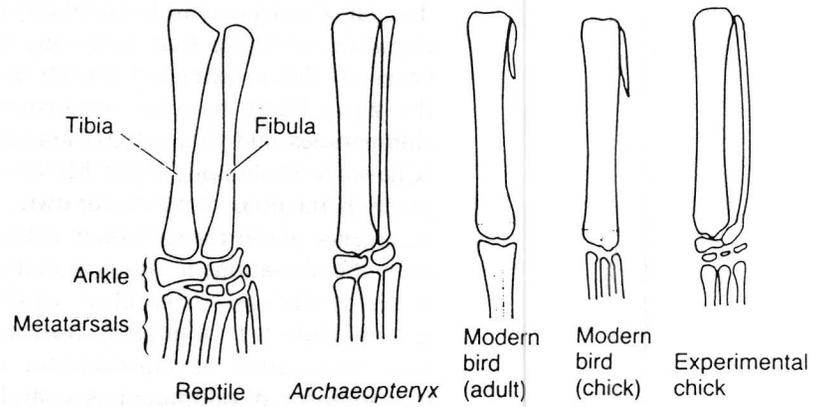


Figure 18.2. Hampé (1960) discovered that if the fibula of the developing chick embryo is prevented from touching the tibia, the fibula grows to its full length, inducing the tarsal bones to develop independently from the tibia, thus resulting in a pattern strikingly reminiscent of the ancestral condition found in the first bird, *Archaeopteryx*. These experimentally produced metatarsal bones are presumed to be homologous to the ancestral metatarsals of *Archaeopteryx*. (Figure from Hampé, 1960).

of this mode of evolutionary change. One is that mutations that reverse a heterochronic shift that originally resulted in the elimination of an ancestral trait should ultimately result in the reemergence of the trait that is presumed to have been present in the phyletic ancestor of the lineage in question (Buss, 1987). In more general terms, the work of embryologists such as Hampé (1960) reveals that experimental perturbations that mimic the emergence of natural variants can result in the reappearance of ancestral traits as well.

The “loss” of self-recognition in gorillas: The heterochrony hypothesis

Understanding the atavistic implications of heterochrony places in an entirely different light recent evidence that gorillas may have undergone a heterochronic shift in the onset of locomotion relative to their acquisition of particular cognitive structures (Antinucci, 1989, Chap. 6). This finding is consistent with several lines of evidence suggesting that the developmental schedules of gorillas are accelerated relative to chimpanzees and orangutans in several domains such as age at weaning, age at first labial swelling, age at menarche, and age at first birth (see Watts & Pusey, 1993). In terms of physical growth in body size, gorillas are sequentially accelerated relative to chimpanzees, whereas humans are sequentially hypermorphic relative to chimpanzees (for an overview see McKinney & McNamara, 1991). That is, gorillas grow faster in each maturation phase than do chimpanzees; humans, in contrast, grow at the same rate as chimpanzees, but stay in each growth phase for a longer period by delaying the termination of each growth phase. It is possible that the gorilla’s accelerated sexual and physical maturation (especially in the

domain of independent locomotion) may interfere with future maturation in cognitive structures that were only allowed for in the great apes and their ancestors due to extended periods of immature development. This seems all the more likely because sensorimotor intelligence in apes (at least, in chimpanzees and orangutans) appears not to close until 6–8 years of age (Chevalier-Skolnikoff, 1983; Mathieu & Bergeron, 1981; Mignault, 1985), precisely the point at which our own research has detected the developmental emergence of self-recognition in chimpanzees (Povinelli et al., in press). Thus, dramatic alterations in physical maturation schedules prior to this point (as is clearly the case in gorillas), could be expected to affect later cognitive growth. Note that in humans, however, selection seems to have favored the early maturation of sensorimotor development. In humans, Stage 6 of sensorimotor development is complete by 18–24 months, but sequential hypermorphosis does not begin to become evident until well after that time (McKinney & McNamara, 1991).

Of course, this specific explanation need not be correct for the general point to be valid: Specific changes in the onset and timing (heterochronic shifts) of particular cognitive pathways may have led to the secondary loss of self-recognition in gorillas. If true, then Patterson's (1984) observations of self-recognition on the part of her home-reared gorilla that had been instructed in a variety of cognitive tasks since 1 year of age, are potentially understandable as an example of the reappearance of ancestral characteristics following perturbations in development. In this case, the experimental perturbation has taken the form of a potentially profound disturbance involving intensive tutoring on a variety of cognitive tasks not found in normal gorilla ontogeny (Patterson & Linden, 1981). It should be emphasized that I do not believe that this is language training per se, but rather aspects of cognitive stimulation related to the construction of a sense of personal agency.

In short, the general hypothesis I am advancing is that psychological ontogeny need not, and indeed, should not, be thought of in fundamentally different terms than morphological ontogeny (see also McKinney & McNamara, 1991). Because the development of the brain (like other morphological structures) is guided by epigenetic interactions, strong environmental inputs during ontogeny may affect psychological ontogeny in the same manner as morphological ontogeny, and thus result in the reappearance of psychological traits that have apparently been "lost" during evolution. To accept the hypothesis as having potential merit, several assumptions need to be made. These assumptions are widespread, but they ought to be made explicit in order for the strengths and weaknesses of the hypothesis to be fully appreciated. First, I assume that phyletic differences in cognitive capacities are the result of the evolution of distinctive neural structures. Second, I assume that the ontogeny of psychological capacities are marked by maturation of brain structures. Of course, these latter developmental changes may range from the dramatic (such as increases in the size and complexity of the frontal cortex) to the subtle (complex readjustments of the physiological strength of neural

networks underpinning particular representations of reality). The final assumption is that normal epigenetic interactions guide the development of brain structures. All of these assumptions seem reasonable, and many are supported by a variety of lines of evidence.

Summary and predictions

After 15 years of debate concerning the self-recognition capacity of gorillas; it may turn out that many gorillas may still possess the basic underlying instructions for the construction of cognitive structures necessary for self-recognition, but that these instructions have been "turned off" due to heterochronic shifts in other aspects of their development. Experimental interventions, such as those received by Patterson's gorilla, may be capable of reinstating the developmental pathways implicated in the expression of self-recognition. Suarez and Gallup (1981), therefore, might have been correct in arguing that gorillas may "lack some as of yet unspecified neuroanatomical features" implicated in the expression of self-recognition (p. 186). However, it may have been somewhat premature to speculate that the neurobiological explanation for the absence of self-recognition is the same in gorillas and other species that show no evidence for self-recognition (Suarez & Gallup, 1981, p. 186). In the account offered here, the relevant neurobiological differences separating gorillas and these other species from chimpanzees, orangutans, and humans may be quite different given that the nature of the secondary loss in gorillas remains unknown. In addition, Gallup (1985) may have been correct in arguing for the secondary loss of the underlying capacity for self-recognition in the gorilla lineage as well (see also Povinelli, 1987). On the other hand, Patterson (1984), too, may have been correct in observing, "Whatever the explanation for the negative findings of other researchers, we believe that we have definitive proof that self-recognition is not beyond the mental capacity of the gorilla" (p. 3). The hypothesis that I have outlined here bridges the gap between the two sides of this apparent deadlock (see Povinelli, 1991).

A final caveat seems warranted in light of mounting evidence that some chimpanzees may not be capable of self-recognition. Swartz and Evans (1991) have recently published the results of a study in which only 1-3 of 11 chimpanzees showed evidence of self-recognition. As noted previously, my colleagues and I have recently tested 105 chimpanzees ranging in age from 10 months to 39 years of age, and hence have had the opportunity to dissect this issue (and others) in far greater detail. We have found clear developmental evidence for at least two transitions in the chimpanzee's capacity for self-recognition. First, there appears to be a clear transition at around 6-8 years of age: about 5% of young chimpanzees 6 years and younger recognize themselves, as compared to nearly 80% of adolescent/young adults 8-16 years of age. The second transition appears to be a decline with age, so that only about 35% of chimpanzees older than 20 years show evidence of

self-recognition. These subjects have been socially reared and housed, they are wild or captive-born, and mother or nursery-reared. None of these factors appear to have any systematic influence on the probability that an animal will recognize itself (Povinelli et al., in press). Thus, it may turn out that the capacity for self-recognition is polymorphic in chimpanzees; hence, the atavism hypothesis may apply to their species as well, although the heterochronic shift is less pronounced, hence the widespread intraspecies variation.

Elsewhere, we have argued that orangutan populations may be expected to show much higher rates (as well as earlier developmental onsets) of self-recognition than both chimpanzees and gorillas (Povinelli & Cant, 1992). We have hypothesized that evolution of an awareness of personal agency (primitive self-conception) was the result of the evolution of large body size in the arboreal ancestors of the great ape-human clade. In particular, we have argued that a sense of personal agency emerged as a necessary conceptual system for directing slow, cautious clambering through a habitat made fragile by excessive body weights (Povinelli & Cant, 1992). If our assumption is correct that orangutans more closely approximate the locomotor condition of the Miocene ancestor of the great apes, then both gorillas and chimpanzees represent derived conditions, both being far more terrestrial than orangutans, gorillas especially so.

At any rate, the possibility that self-recognition in chimpanzees is more polymorphic than was once assumed in no way invalidates the hypothesis offered here. Indeed, it only adds to the potential ways in which the atavism hypothesis might be falsified. In addition, it provides an opportunity for testing Gallup's (1985) model of the relationship between self-recognition and mental-state attribution using an intraspecies comparison.

Of course, any hypothesis is only as good as the set of falsifiable predictions that it makes. The atavism hypothesis advanced here makes at least two explicit predictions in terms of self-recognition research. First, it predicts that most infant gorillas provided with the cognitive stimulation that Patterson's gorilla received should show evidence of self-recognition. A clear weakness of the hypothesis is that it cannot specify the exact nature of the stimulation necessary, nor can it predict the critical windows of opportunity during ontogeny in which such interventions would produce the ancestral trait. Mitchell (1992, 1993) could argue that the type of tutoring necessary has to do with "body part objectification." However, although the hypothesis outlined here remains silent on what the necessary cognitive structures are that underpin and allow for self-recognition, elsewhere we have argued that it is the development of an awareness of the self as causal agent (a sense of personal agency) (Povinelli & Cant, 1992). Thus, if the general atavism hypothesis is correct, it provides an ideal case for testing these competing explanations of the cause of mirror self-recognition.

The second and potentially more important prediction from the hypothesis is that no amount of similar cognitive training should produce self-recognition in individual members of species outside the great ape-human clade. This

phyletic difference is predicted because these species descended from lineages in which the underlying pathways necessary for the development of the relevant cognitive structures had not yet evolved. For those species (gibbons, Old and New World monkeys, prosimians – perhaps the remaining diversity of life itself) there exists no ancestral trait to reappear. An exception to this prediction would exist if self-recognition itself were produced by a heterochronic shift that could successfully be mimicked by experimental perturbations in, for example, macaque ontogeny, thus resulting in the appearance of “descendant characteristics.”

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