
48 Evolutionary Psychology and Primate Cognition

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Probably, researchers from a greater variety of disciplines study the nonhuman primates than any other group of animals. Primates interest ecologists, zoologists, medical researchers, geneticists, anthropologists, and psychologists, like myself. Since nonhuman primates belong to the same order of mammals as ourselves, their cognitive processes are more likely than those of any other species of animal to be relevant to understanding the remote origins of the human mind.

One might think that this truth has long been generally accepted. Far from it; even today, some would dispute that primate behavior had *any* relevance to the vexed issue of the human mind (Macphail 1998). And in the days when what we would now call “evolutionary psychology” was called “comparative psychology,” psychology did not do itself any favors by its choice of species. Typically, the comparative psychologist studied only a few species: the laboratory (white) strain of the rat; occasionally the ring-tailed lemur; more often, the rhesus monkey and the chimpanzee. It was hard to escape the impression of a natural scale, with each living species a sort of model of an earlier stage in the evolution of the more advanced forms; indeed, for some practitioners, that really seems to have been their underlying theory (for details of this history, see Burghardt 1973; Burghardt and Gittleman 1990). In reality, of course, evolution seldom produces a linear progression. Yet, because comparative psychologists only had access to a restricted range of species handily available in captivity, even those who did not think in linear terms had difficulty convincing anyone that their theories did not retain the long-discredited logic of progressive evolution. Comparative psychology became something of a Cinderella subject in psychology.

Its change in fortune, and the subtle transformation to a properly evolutionary psychology, came with the huge burgeoning of primate field

studies in the 1970s and 1980s. Fieldwork was done for many different purposes, but the growth in knowledge it has produced has at last allowed a genuinely comparative database to be built up. Field primatology began with a few isolated studies of “glamorous” or easy-to-watch species: chimpanzees, baboons, the species of macaque that live as commensals in Japan and India, those South American monkeys that happened to be marooned on Barro Colorado Island by the waters of the Panama Canal. It has grown to the present state in which virtually every branching point on the tree of primate phylogeny has at least one detailed study in the wild, and in some cases every species in a group has been studied.

Theoretical methods have also advanced over the same period, from the early days of two-species or two-population comparisons (see examples in Sussman 1979), to the modern use of quantitative comparisons performed as phylogenetic contrasts (to remove concerns of pseudoreplication resulting from possible phylogenetic inertia) across the whole order (e.g., Barton and Dunbar 1997). It is at last possible to focus clearly on the central questions:

- When did a particular cognitive trait enter the human lineage?
- What was its original adaptive function? (And has it been retained for the same reason, or is it now valuable for some different purpose?)
- What is the cognitive basis for the trait, and how does its organization relate to other mental capacities?

In order to illustrate how these questions may be approached, I use some recent studies of monkeys and great apes.

It would be relatively straightforward to establish when a trait originated if its presence or absence could be clearly identified in living species. Unfortunately, definitive evidence of the *absence*

of a cognitive trait is often difficult to obtain, and we may have to be content with a surrogate measure and a residual level of uncertainty.

Monkeys and apes have long been known to show social manipulations that appear complex and clever to human observers: third-party support to win resources, ruses that rely on deception, long-term nurturing of friendships and reciprocal collaboration, targeted choice of allies and repair of disrupted relationships, and so on (see papers in Byrne and Whiten 1988; Harcourt and de Waal 1992). In contrast, people who study lemurs and lorises, or indeed most other mammals, report nothing very similar. Moreover, the simian primates (monkeys and apes) have unusually large brains for animals of their size (Jerison 1973; Passingham 1981); lemurs and lorises, on the other hand, have brains of more typical size for mammals. This difference is principally expressed in neocortical volume, and there is a direct relationship between neocortical volume and the amount of “clever-looking” behaviors that researchers observe. That applies to deception, to innovation, and to tool use (Byrne 1996b; Reader and Laland 2001). At least in the case of deception, this is not a by-product of the greater opportunities for researchers to see an interesting behavior if they watch a larger social group because the effect is independent of group size. In modern primate phylogeny, which is based on the pattern of differences in species’ DNA, the monkeys and apes form a monophyletic clade; that is, they are a group descended from a single ancestor species. Because some fossils are available for calibrating the evolutionary tree revealed by molecular study, we can approximately date this ancestor species as living 30 million years ago. For these reasons, we know that the mental capacity to use other social individuals in a manipulative, clever-seeming fashion, including quite elaborate cooperation and the use of deceptive tactics, has a rather ancient origin in the human lineage (Byrne 1995, 2000).

The answers to functional questions are always more open to debate than matters of dating. No

modern monkey is “equivalent” to the ancestors of monkeys and apes living of 30 million years ago; there is no model of this extinct form. We cannot therefore study the original function of the enlarged simian neocortex. It is evident that all modern simians benefit socially from the cooperation and competition that their clever-looking behavior allows, but would they perhaps cope perfectly well without it if they could not afford large brains? In metabolic terms, brain tissue is the most “expensive” tissue in the entire body (Aiello and Wheeler 1995; Armstrong 1983); and uniquely, brain tissue remorselessly requires a constant energy supply or it deteriorates. Other things being equal, having a *smaller* brain is a good thing, so some positive advantage of brain enlargement must exist in every case where we find species with relatively large brains.

In fact, there is evidence that a large neocortex confers social benefits on modern monkeys and apes. The average group size in which they live is well predicted by the degree of their neocortical enlargement (Barton and Dunbar 1997; Dunbar 1992). On the other hand, measures of environmental complexity, such as range size and the distance of a day’s journey (when corrected for the body size of the species concerned), do not correlate with neocortex size. Furthermore, in Old World monkeys and apes, which use grooming to build up friendly social relationships, the typical group size also predicts the amount of grooming seen; in a large group, more grooming is apparently necessary.

Although all these relationships are correlational, the associations between neocortex size and both a method of building up social relationships (grooming) and the frequency of use of a social tactic (deception), encourage the Machiavellian intelligence hypothesis: that an important selective pressure on the evolution of intelligence has been social complexity (Byrne 1996a; Humphrey 1976; Jolly 1966). The fact that the group sizes of modern primate species relate to their neocortex volumes suggests that social complexity may set an approximate upper limit on

group sizes because of the demands that it places on the limited neocortex tissue available. Over longer time scales, pressure to live in ever-larger groups is felt as positive selection for an enlarged neocortex.

The benefits of a large neocortex—the underlying cognitive basis of monkey and ape social sophistication—are not easily determined. It is tempting, but it may be utterly wrong to assume that an animal that works over many months to build up a friendly relationship with another has some idea of the effect its behavior is having on the mind of the other. (“If I scratch his back often, he’ll like me,” rather than simply “If I scratch his back often, he’ll probably scratch mine one day.”) We also readily assume that an animal that uses a trick that relies on successful deception to gain some special resource actually meant to do so (i.e., it planned the effect of its actions in advance). That is, we assume the agent realizes that by producing a false belief in its victim, it may have risked losing a friend or gaining an enemy. The alternative explanation is that such behavior is a more prosaic mixture of genetic predispositions and rapid learning; often this is more likely.

Baboons, for example, are famous for building up long-term friendships that result in the benefits of social support on later occasions (Smuts 1983; Strum 1983). When these apparently important relationships are threatened by conflict, the baboons show behavior described as reconciliation (Castles et al. 1999; de Waal and van Roosmalen 1979). In this, friendly acts are actually more likely after a fight than before; however, as far as we know, all baboons will show these behaviors under the appropriate circumstances. They apparently do not have to be learned or deduced. So it is entirely possible that the baboon is genetically equipped with tendencies to direct affiliative acts to high-ranking members of its social group and to respond positively to affiliation shown by others, both at the time and afterward.

The underlying cognition needed to make these traits “pay” is rather simple. Baboons must

recognize others as individuals and must be able to categorize those individuals by their dominance rank. They must also be able to categorize individuals by their past history of showing affiliative or aggressive acts toward themselves; for this, a single dimension would suffice, which we might call “self-friendliness.” The genetic tendency of working to increase the level of self-friendliness in dominant members of the groups would automatically produce much of the social engineering we know from Old World monkeys like the baboons. Even reconciliation would follow, provided the animals are equipped with a tendency to show affiliation to dominant individuals whose self-friendliness has recently decreased. Simple rules of this sort would rapidly pay in evolutionary currency and are exactly what we would expect to evolve in highly social species.

Some of the “clever” behaviors of baboons, such as deception or innovation, are by no means universal; they are relatively rare, and each case is idiosyncratically different (Byrne and Whiten 1985). These are hallmarks of learning or deduction, but once again, they may not require any deep analysis of the social situation. Consider, for instance, a baboon that leaped to its hind legs and scanned the distance, for all the world as if it had seen a predator or an unexpected incursion of another baboon troop, at precisely the moment when it was being attacked by a dominant. Convenient? Indeed so; the attack was aborted, and no baboon troop or predator ever materialized. Yet this tactic may depend on no more than rapid learning. All that is required is a little history, in which perhaps the same baboon once actually did see a predator at a time when it was losing a fight and as a result was not thrashed (Byrne 1997). Avoidance of pain can function as a reward, making any preceding behaviors more probable in future similar cases. In this case, the preceding behaviors were leaping to the hind legs and scanning the distance. Learning must be rapid, but social insight may be lacking.

Innovations, likewise, are impressive and memorable if they happen to be beneficial and become enshrined traditions, but most primate researchers have seen oddities of behavior or fads that are pointless and simply die out. It is therefore quite possible that successful innovation depends on no more than rapid learning and a bit of luck, but lacks insightful understanding of the mechanism of the benefit conferred (Kummer and Goodall 1985). For example, Mike, one of the Gombe chimpanzees, discovered that banging empty kerosene cans together could help his rise in social dominance. Yet this device was not used by others at Gombe, suggesting that the chimpanzees were unable to understand the mechanism of Mike's good fortune.

Researchers have to be very cautious, then, in attributing to nonhuman primates the ability to understand social behavior or how things work in the mechanistic way that adult humans understand them. Rapid learning in social circumstances, a good memory for individuals and their different characteristics, and some simple genetic tendencies, can explain much that has impressed observers as intelligent behavior in simian primates. Is that all there is to be discovered? I believe not, but my confidence comes from the study of something rather less glamorous than social manipulation: feeding.

For most species of primates—monkeys, lemurs, and lorises—the challenge of feeding is largely a matter of getting to food (Byrne 1999a). Food may be scarce, dispersed, or concealed, but once it is at hand, eating is simple. [Interesting exceptions to this generalization occur in some lemurs, for instance, the aye-aye (*Daubentonia*), which uses echolocation to detect grubs in rotting wood and specialized teeth and finger adaptations to get them out (Erickson 1991); and the bamboo lemurs (*Hapalemur*), which use a highly specialized manual technique to eat the giant grasses they subsist on (Stafford et al. 1993).] However, in the great apes, remarkable feeding techniques are found that closely match the physical problems presented by local food sources. In chimpanzees, tool-making

and tool-using traditions vary from site to site (McGrew et al. 1979), and in gorillas, complex manual techniques are found that are specific to a number of different plants found only in the range of a few dozen groups of gorillas (Byrne and Byrne 1991, 1993; Byrne et al. 2001). Evidently great apes are able to learn elaborate techniques to solve manual problems.

A number of facts support the hypothesis that great apes can learn manual techniques by imitating the underlying structure of a behavior, filling in the details of execution in the most convenient way, often by trial and error (Byrne 1993; Byrne and Russon 1998). Although they are efficient and highly standardized in overall form in the local population, the gorillas' techniques are not the only, or the simplest, ways of obtaining the plants. One chimpanzee tool-using technique actually exists in two variants at different sites, even though the ant species, and the twigs used to make the tools, are available at each site. At Gombe, Tanzania, ants are collected on a large, stripped wand and scooped into the mouth in a ball (McGrew 1974); at Taï, the Ivory Coast, ant dipping is done with one hand, using a shorter stick that often has a frayed end (Boesch and Boesch 1990; see also Whiten, chapter 47 in this volume). The second method is less efficient, yet the Ivoirean chimpanzees have not discovered a better way. In both gorillas and chimpanzees, injuries from snares often maim the hands of exploring, curious infants and young juveniles. Surprisingly, individuals can survive with highly disabling hand injuries, even though they rely on complex manual techniques to feed on some important resources. Rather than growing up to acquire novel techniques that are specialized for making the most of the remaining manual function, these animals learn the same methods as able-bodied individuals and work around their own disabilities by using other limbs, fingers, chin, or branches to carry out the same process (Stokes and Byrne 2001).

To learn the organization of behavior imitatively, it is first necessary to “see” that organization—to go beyond the surface level in

which behavior consists of fluid movement and reach the underlying structure. Judging by the great apes' skills, that will include recognizing the modular grouping as well as the linear sequence of actions, the coordination of the two hands (and sometimes mouth as well) used in different, complementary roles, and the use of some modules as subroutines in the service of the overall routine. As with the social skills of monkeys, this may not imply a deep understanding of mechanism. All these aspects of behavior produce distinctive traces in behavior, provided the observer can repeatedly watch the skill in action (Byrne 1999b). On the other hand, the ability to see the underlying modularity, hierarchical organization, and coordination of effectors is an essential starting point for understanding cause and effect and the purposes that lie behind an action. So it may be that the great apes' efforts at eating their more awkward foods will give important clues to understanding the evolutionary origins of the human capacity to understand causes and intentions.

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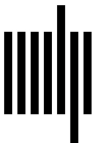
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