

What are big brains for?

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An article in this issue of PNAS by Reader and Laland (1) offers a novel answer to the question “Why do primates have such big brains?”

Across the animal kingdom, brain size increases with increasing body size. Despite this common scaling principle, however, brain size to body weight ratios differ from one taxonomic group to another (2). In primates, for example, the brains of apes are generally larger relative to body weight than the brains of monkeys, whereas the brains of monkeys are larger than those of prosimians (2). Structural differences are also apparent. In chimpanzees, a larger proportion of the brain is devoted to neocortex than in monkeys, who in turn have proportionately more neocortex than prosimians (3, 4). Within the neocortex, ape (and especially human) brains have a particularly enlarged prefrontal cortex, an area known to be involved in many forms of abstract thought and rule learning (5, 6).

Increases in the size of primate brains have come despite the fact that brain tissue is metabolically very costly (7). What selective pressures have overcome these costs? When the question is applied to humans answers typically refer to the adaptive advantages of technology (initially, stone tools) and language. But monkeys and apes use only rudimentary tools and lack language entirely, yet their brains are significantly larger than those of similar-sized mammals. Some other selective pressures must be at work.

Among primates, relative brain size (corrected for body weight) is greater in species with larger home ranges and greater in species that are fruit-eating or omnivorous than in species that eat leaves (8). Species that feed on fruit may face special problems in learning and memory because they depend on widely spaced food that is ephemeral in both space and time (9, 10).

In contrast to this “ecological” explanation of brain evolution, others suggest that primate brains have evolved primarily to deal with social problems. Primates, they argue, live in relatively large groups where an individual’s survival and reproductive success depends on its ability to manipulate others within a complex web of kinship and dominance relations (11–

13). In recent years this “social intelligence” hypothesis has received two sorts of empirical support.

First, several authors have shown that, in both primates and carnivores, neocortex size is positively correlated with group size, independent of a species’ home range size (14). Group size is here taken as a “proxy for social complexity.”

Second, Harcourt (15, 16) found that primates do indeed differ from most other species in at least one measure of social complexity, patterns of alliances. Alliances occur whenever two animals, A and B, are involved in an aggressive encounter and a third, C, joins the fight in support of one of them. An alliance may be formed spontaneously, or it may occur only after C has been solicited by A or B. Alliances occur in many species, primarily among close relatives. Only primates, however, form their alliances “strategically,” selectively soliciting support from some individuals more than from others. And only primates compete to establish close bonds with particular powerful partners (16). In many species, for example, animals compete to form bonds with the highest-ranking individuals and preferentially solicit as allies those who rank higher than both themselves and their opponent (17–19). To solicit partners in this way, an individual must know not only its own relative rank but also the rank relations that exist among others. Such “triadic” knowledge can be obtained only by observing interactions in which one is not involved and making the appropriate deductions (20). Moreover, as group size increases, the need for triadic knowledge places increasing demands on individuals, because larger groups produce an explosive growth in the number of triadic relations (21). If primates are, in fact, unique in forming strategic alliances, and if strategic alliances require knowledge of the relations that exist among others, then the social competition found in large groups offers one explanation—unrelated to tools or language—for primates’ unusually large brains.

The purported link between brain size and ecological or social intelligence is, however, entirely conjectural. We may assume that memorizing the location of ripe fruit or remembering the kin rela-

tions of ones’ opponents demand considerable brainpower, but this assumption is neither supported nor refuted by any widely accepted evidence. Perhaps more important, the “intelligence” of different species is notoriously difficult to compare. Different species manifest their intelligence in different ways, making it almost impossible to find an objective measure of intelligent performance that can be used across many taxa (22).

In the current issue, Simon Reader and Kevin Laland (1) offer a novel approach to research on brain and intelligence in primates. Following the pioneering work of Lefebvre *et al.* (23) on birds, Reader and Laland searched all of the major primate journals for evidence of innovation (defined as apparently novel solutions to environmental or social problems), social learning (the acquisition of information from others), and tool use. They assumed that the frequency of such behaviors, appropriately corrected for the amount of time that had been devoted to studying each species, would provide a useful measure of a species’ behavioral flexibility, and that behavioral flexibility was a good measure of intelligence.

Once they had accumulated data on innovation, social learning, and tool use from 116 primate species, Reader and Laland tested whether the frequency of such behavior was correlated with brain size. They found significant, positive correlations between brain size and all three behaviors.

Reader’s and Laland’s results offer a new perspective on the social intelligence hypothesis because they found no significant relation between group size and the frequency of social learning. Natural selection may, therefore, have favored an increase in brain size because of benefits derived from innovation or social learning that are independent of a species’ typical group size. Reader’s and Laland’s analysis also reminds us that ecological and social intelligence are difficult to distinguish in present-day species and unlikely to have played entirely separate roles during evo-

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lution. Social learning, after all, often helps individuals to acquire food, whereas tool use can have social as well as ecological benefits [recall Jane Goodall's (24) description of a male chimpanzee who rose in rank when he learned to bang together garbage can lids in dominance displays]. Finally, Reader and Laland found no support for the hypothesis that innovation and social learning are independent processes that require distinct psychological abilities (25). To the contrary, the frequencies of innovation, social learning, and tool use all were highly correlated across species.

Debates about the evolution of intelligence are sure to continue after these important new results. For cognitive scientists concerned more generally with the relation between brain and behavior, two problems seem particularly intriguing. The first concerns the role of language. For much of its young history, the field of cognitive science has focused almost exclusively on human cognition and the relation between language and thought, without paying much attention to the nature of thought in species where language is absent. Human brains, however, have not become large *de novo*; instead, they are at least partly the result of a general

increase in brain size that occurred in many primate species—especially apes—during a time when language was not present. The selective forces that favored large brains before language evolved may be just as important in understanding human cognitive skills as the selective forces at work after language appeared.

The second problem concerns the puzzle of modularity. Some human skills (face recognition and language learning, for example) seem to emerge in highly predictable ways despite wide variations in environment and appear to be controlled by specific, narrowly defined areas of the brain. These observations have led some to argue that the brain is organized into “modules” (26), all joined to a central processing system that organizes modular input to produce higher-order mental activities like problem solving and decision making. Others (27) disagree, believing that the apparent modularity of human intelligence reveals more about our ignorance of the brain than about our understanding of how it works.

For ethologists studying animals in their natural habitats, the notion of modular intelligence hardly comes as a surprise. Specialized, domain-specific performance almost seems the rule rather than the

exception. Arctic terns migrate each year from one end of the earth to another, *Cataglyphis* ants navigate across featureless deserts, bees dance to signal the location of food, and some corvid species hide thousands of seeds in the fall, recovering them with unerring accuracy throughout the winter; yet despite these specialized skills we don't think of terns, ants, bees, or crows as generally more intelligent than other species. They are, instead, more like nature's idiots savants.

Nonhuman primates, on the other hand, are beginning to confound those who believe that animal intelligence is always modular. As Reader's and Laland's results indicate the behaviors that make monkeys and apes seem intelligent—innovation, social learning, and tools—are not easily placed in any one, clearly delineated domain. True, there is strong support for the social intelligence hypothesis, but the social domain of primates is much harder to define than domains of expertise like the tern's skills in navigation or the bee's skills in communicating about food. The primate brain may indeed have a modular flavor to it, and primates may indeed be at their most impressive when dealing with social problems. The extent and limits of social intelligence are, however, fuzzy.

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