

Evolution in the Social Brain

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The evolution of unusually large brains in some groups of animals, notably primates, has long been a puzzle. Although early explanations tended to emphasize the brain's role in sensory or technical competence (foraging skills, innovations, and way-finding), the balance of evidence now clearly favors the suggestion that it was the computational demands of living in large, complex societies that selected for large brains. However, recent analyses suggest that it may have been the particular demands of the more intense forms of pairbonding that was the critical factor that triggered this evolutionary development. This may explain why primate sociality seems to be so different from that found in most other birds and mammals: Primate sociality is based on bonded relationships of a kind that are found only in pairbonds in other taxa.

The brain is one of the most expensive organs in the body, second only to the heart: The brain's running costs are about 8 to 10 times as high, per unit mass, as those of skeletal muscle (1, 2). Although the brain's ability to control the body's functions is obviously useful, it entails something of an evolutionary puzzle. The neurobiologist Harry Jerison first pointed this out during the 1970s (3), when he drew a distinction between the component of the brain required to meet the body's physical needs and the component that was left over, which could attend to tasks of a more cognitively complex nature. This second component of the brain has been increasing over evolutionary time across the birds and mammals, but fish and reptiles continue to thrive with brains of very modest size. Although it is easy to understand why brains in general have evolved, it is not so obvious why the brains of birds and mammals have grown substantially larger than the minimum size required to stay alive.

Traditional explanations for the evolution of large brains in primates focused either on ecological problem solving or on developmental constraints. Early studies identified physiological and life-history traits—including large body size, metabolic rates, and prolonged development—that were associated with large brains (4, 5). Some argued that this correlation was due to the more efficient metabolism of larger-bodied animals, which allowed more energy to be devoted to fetal brain growth and thereby made the evolution of larger brains possible (6, 7). All else being equal, big brains are a useful if unintended by-product of efficient energy use. In addition to this theory, some evidence supported ecological problem-solving as a possible explanation: Among primates, for example, large-

brained species have larger home ranges (perhaps requiring more sophisticated mental maps), and frugivores have larger brains than folivores (fruits are much less predictable in their location and availability than leaves) (8).

On closer examination, most of the energetic explanations that have been offered identify constraints on brain evolution rather than selection pressures. In biology, constraints are inevitable, and crucial for understanding evolutionary trajectories, but they do not constitute functional

brain evolution against the steep selection gradient created by the high costs of brain tissue. In this respect, most of the ecological hypotheses proposed to date also fail. None can explain why primates (which have especially large brains for body mass, even by mammal standards) need brains that are so much larger than, say, squirrels, to cope with what are essentially the same foraging decisions.

As an alternative, Byrne and Whiten proposed the Machiavellian Intelligence hypothesis (9) in the late 1980s: They argued that what differentiates primates from all other species (and, hence, what might account for their especially large brains) was the complexity of their social lives. Unfortunately, the term "Machiavellian" was widely interpreted as implying deceit, manipulation, and connivance—traits that most people were reluctant to attribute to any species other than humans. In fact, although these are potential aspects of social complexity, they did not lie at the heart of Byrne and Whiten's proposal. Instead, the proposal emphasized the complex social environments in which primates lived. The less contentious label social brain hypothesis (SBH) (10, 11) has thus been adopted.

Although initially criticized for being conceptually vague, the SBH eventually began to receive increasing quantitative support. A series of studies demonstrated that, among primates at least, relative brain size [usually indexed as relative size of the neocortex, the area that has disproportionately expanded in primates (12)] correlates with many indices of social complexity, including social group size (Fig. 1) (13), number of females in the group (14), grooming clique size (15), the frequency of coalitions (16), male mating strategies (17), the prevalence of social play (18), the frequency of tactical deception (19), and the frequency of social learning (20).

A weakness of most analyses, however, is that they invariably test a single hypothesis without ensuring that the same predictions could not also arise from other equally plausible explanations. Although some attempts have been made to discriminate between ecological and social theories (13, 21), and these have largely supported the social hypothesis, there has been little effort to develop an explanatory framework that integrates the many social, ecological, and life-history correlates of brain size that have been identified. As a result, constraint-type explanations (e.g., correlations with life history)

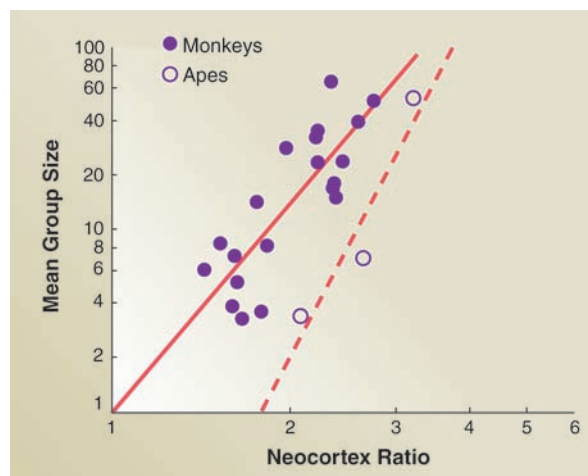


Fig. 1. In anthropoid primates, mean social group size increases with relative neocortex volume (indexed as the ratio of neocortex volume to the volume of the rest of the brain). Solid circles, monkeys; open circles, apes. Regression lines are reduced major axis fits. [Redrawn from (47)]

explanations—that is, just because a species can afford to evolve a larger brain does not mean that it must do so. Proponents of developmental explanations seem to have forgotten that evolutionary processes involve costs as well as benefits. Because evolution is an economical process and does not often produce needless organs or capacities, especially if they are expensive to maintain, it follows that some proportionately beneficial advantage must have driven

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have continued to be emphasized as though they were alternative explanations for evolutionary function.

Social Brain, Social Complexity

The broad interpretation of the social brain hypothesis is that individuals living in stable social groups face cognitive demands that individuals living alone (or in unstable aggregations) do not. To maintain group cohesion, individuals must be able to meet their own requirements, as well as coordinate their behavior with other individuals in the group. They must also be able to defuse the direct and indirect conflicts that are generated by foraging in the same space.

Appreciating that the problem to be solved lies at the level of the group (i.e., the need to maintain group coherence through time) and not just at the level of individual foraging strategies might allow us to reconcile the apparent conflict between the ecological and social hypotheses. One example of this apparent conflict is the suggestion that flexibility of foraging skills might be more important than social skills. The evidence that brain size correlates with technical innovation and the acquisition of new food sources through social learning (or cultural transmission) in both birds (22) and primates (20) supports this claim. However, in the final analysis, all of these hypotheses (social and ecological alike) are at root ecological: They allow animals to survive and reproduce more effectively. The SBH proposes that ecological problems are solved socially and that the need for mechanisms that enhance social cohesion drives brain size evolution. In contrast, the more conventional ecological hypotheses assume that animals solve these same ecological problems individually by trial and error learning and do not rely on any form of social advantage.

For primates at least, sociality is specifically driven by the need to minimize predation risk (23–25). However, we have shown that two different kinds of predators (chimpanzees and felids) from five different ecological communities on two continents differentially select small-brained prey species (relative to their availability in the population) when we control for other traits (including group size) (26). Predation thus acts directly and indirectly (by means of group size) on brain evolution. Nonetheless, whatever its advantages, group living incurs substantial costs, both in terms of ecological competition and, for females, reproductive suppression (23, 24). Hence, behavioral flexibility within a social situation may be essential for individuals to make the most of sociality. For anthropoid primates, this behavioral flexibility is in part reflected in the use of intense social bonds (often, but not always, serviced by social grooming) to prevent groups from disintegrating under these pressures (15).

The net consequence of these kinds of pressures is that species that evolve larger brains ultimately have higher fitness. Jerison (3) himself pointed out that, in the Paleolithic record, increases in brain size among carnivores and their prey species (mainly ungulates) seem to track each other closely over time, with ungulate brain size leading. These findings are interesting in themselves and also mesh well with findings that brain size can be associated with other types of ecological flexibility—for

more widely, and several attempts have been made to extend the hypothesis to nonprimate taxa, including ungulates (29, 30), carnivores (31), bats (32), and even birds (33), albeit with somewhat mixed results. Indeed, several studies have argued that sexual selection rather than sociality might be a more important factor driving brain evolution (32, 34). Yet evidence shows that the correlation is the reverse of what one might expect (polygamous species actually have the smallest brains), making

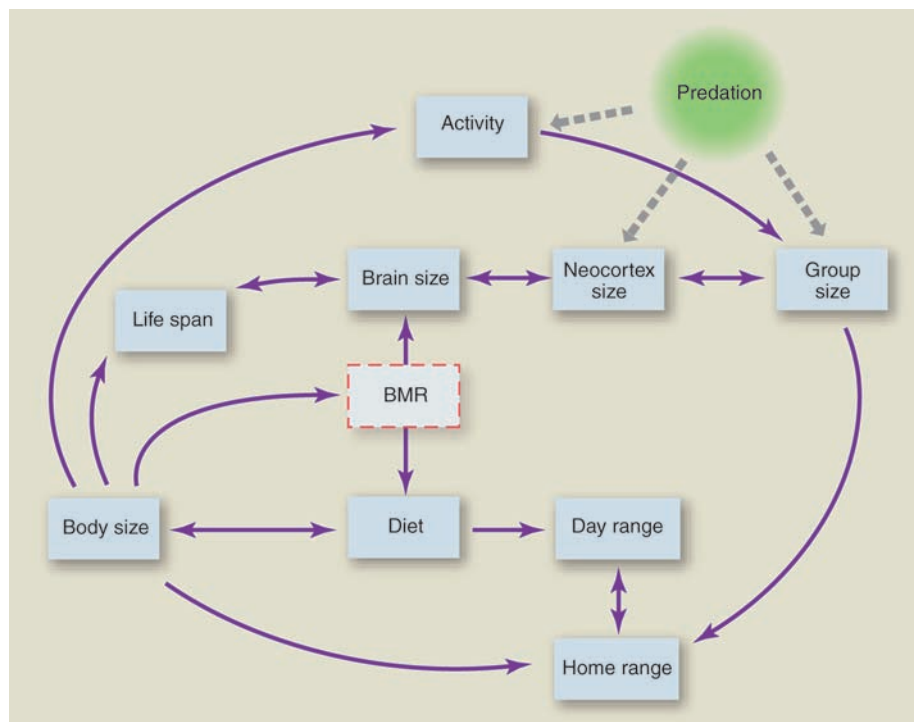


Fig. 2. Path analysis of correlates of brain size in primates. The best model for group size included just three variables (neocortex size, activity, and range size). Factors that are more remote in the path diagram provide a significantly poorer fit, suggesting that they act as constraints rather than driving variables. BMR, basal metabolic rate. [Reproduced with permission from (16)]

example, that brain size is a predictor of both extinction risk and invasion success in birds (27, 28).

To tease out the relationship between the nexus of factors that correlate with brain size, we have recently undertaken path analyses of primate and bird data to identify causes, consequences, and constraints in brain evolution (16). These analyses demonstrate not only that energetics (i.e., ecology) and life history impose constraints on brain size (such that these constraints require solutions if a species is to evolve a substantially larger brain) but also that the key selection pressure promoting the evolution of large brains is explicitly social (Fig. 2).

Brain Evolution in Birds and Mammals

Although the SBH was originally conceived for primates, the same principle could apply

sexual selection an unlikely suggestion, although it may influence some components of the brain [such as the limbic system in male primates (35, 36)].

Although it is possible that the SBH applies exclusively to primates, biologists are usually reluctant to argue for special cases. Fortunately, the recent availability of more powerful statistical tools has allowed us to resolve this enigma. First, we have shown that there is a strong co-evolutionary relationship between relative brain size and the evolution of sociality from an asocial (or less social) state in primates, ungulates, and carnivores (31). Second, for four orders of mammals (primates, bats, artiodactyl ungulates, and carnivores) and 135 species of birds representing a wide cross-section of avian orders, we have shown that, in all taxa except anthropoid primates, the relationship between brain size and sociality is qualitative and not

Social Cognition

quantitative: In each case, large relative brain size is associated explicitly with pairbonded (i.e., social) monogamy (Fig. 3).

These findings suggest that it may have been the cognitive demands of pairbonding that triggered the initial evolution of large brains across the vertebrates. More important, pairbonding is the issue, not biparental care. This is obvious in the case of ungulates: Biparental care does not occur at all in this taxon, yet ungulates that mate monogamously have substantially larger brains than those that mate polygamously (Fig. 3).

How Complex Can Pairbonds Be?

The important issue in the present context is the marked contrast between anthropoid primates and all other mammalian and avian taxa (including, incidentally, prosimian primates): Only anthropoid primates exhibit a correlation between social group size and relative brain (or neocortex) size. This quantitative relationship is extremely robust; no matter how we analyze the data (with or without phylogenetic correction, using raw volumes, or residuals or ratios against any number of alternative body or brain baselines) or which brain data set we use (histological or magnetic resonance imaging derived, for whole brain, neocortex, or just the frontal lobes), the same quantitative relationship always emerges. This suggests that, at some early point in their evolutionary history, anthropoid primates used the kinds of cognitive skills used for pairbonded relationships by vertebrates to create relationships between individuals who are not reproductive partners. In other words, in primates, individuals of the same sex as well as members of the opposite sex could form just as intense and focused a relationship as do reproductive mates in non-primates. Given that the number of possible relationships is limited only by the number of animals in the group, primates naturally exhibit a positive correlation between group size and brain size. This would explain why, as primatologists have argued for decades, the nature of primate sociality seems to be qualitatively different from that found in most other mammals and birds. The reason is that the everyday relationships of anthropoid primates involve a form of “bondedness” that is only found elsewhere in reproductive pairbonds.

This suggestion merely adds to the puzzle of social bonding. What is it about social bonds that is cognitively so demanding? There seem to be two obvious possibilities in the case of reproductive pairbonds. One is that lifelong monogamy is a risky commitment; to avoid the risk of bearing a disproportionate share of the costs of reproduction, individuals must be especially careful in choosing good-quality (i.e., fertile) mates who will be reproductively loyal and play their full role in the processes

of rearing. The other possibility is that a working reproductive relationship that involves substantial postnatal parental investment requires very close coordination and behavioral synchrony; if successful rearing requires both partners to invest time and energy in the rearing process, then the pair needs to regulate its activities so that each has enough time for feeding and rest. That will usually necessitate some degree of activity synchronization—in some cases, to ensure the pair do not drift apart as a result of different activity schedules, and in other cases, to ensure that rearing or

Part of the problem here is that social relationships have been seen as mere epiphenomena spawned by the issues of real biological interest, namely mate choice and parental investment. The social learning version of SBH (20, 22) inherits a sense of that assessment: Sociality is of interest only in so far as it provides a context in which animals can acquire foraging information that has immediate benefits for them in terms of individual fitness. However, this misses the point of primate sociality—indeed, the nature of sociality, and especially pairbonding—in all higher vertebrates. In these intensely social spe-

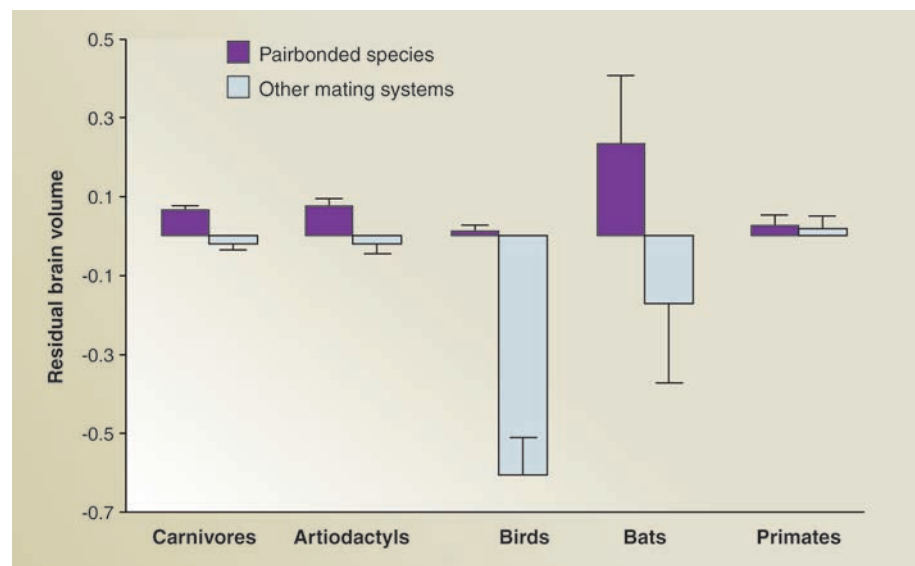


Fig. 3. Mean (\pm SE) of residual brain volume (controlling for body size and phylogeny) in species with pairbonded (purple bars) versus all other mating systems (gray bars) in birds and four orders of mammals. The differences are significant in all cases except primates.

vigilance duties are time-shared appropriately (37). Which of these two has been the key driver for brain evolution, or whether both have been equally important, remains to be determined.

It has become apparent that we lack adequate language with which to describe relationships, yet bondedness is precisely what primate sociality is all about. Intuitively, we know what we mean by bondedness because we experience it ourselves, and we recognize it when it happens. The problem, perhaps, is that bondedness is an explicitly emotional experience and language is a notoriously poor medium for describing our inner, emotional experiences. Because relationships do not have a natural objective cognitive dimension that we can easily express in language, comparing the bondedness of different species is difficult (this may also explain why ethologists have invariably ducked the problem completely, preferring observable descriptions of behavior to grappling with what is going on inside the animal).

cies, social relationships are not so much an emergent property of mating and parenting strategies as the means to achieving those strategies. A group of this kind is an implicit social contract: To form a group that provides a benefit of cooperation (for example, reducing predation risk), members are necessarily obliged to trade off short-term losses in immediate benefits in the expectation of greater gains in the long term through cooperation. Fitness payoffs are determined not by an individual's immediate “here-and-now” personal fitness, but by the extent to which the group can generate longer-term payoffs for the individual. In effect, we are dealing explicitly with multi-level selection and the long-overlooked topic of niche construction (38). Once we understand this, the reasons why animals should invest in relationships become clear. Relationships provide the key to fitness benefits at the group level, and the “trickle-down” benefits are reaped by the individual (39). An individual will be prepared to invest in social strategies that create groups if, by doing so, it gains higher net

fitness (i.e., at the end of its lifetime) than pursuing more individualistic strategies.

What Microneurobiology Has to Tell Us

There has, of course, been growing interest in recent years in some of the neurobiological correlates of social bonding. Particular interest has focused the role of oxytocin (and its male equivalent, vasopressin) in pairbonded species (40), but other neuropeptides have also been identified as playing an important role in social bonding [e.g., endorphins (41)]. In addition, a parallel interest has been developing in the role of several specific neuronal assemblages, including mirror neurons (42) and so-called spindle cells in the anterior cingulate cortex (43), as well as in specific genes such as *GLUD2* [a retro-gene, derived from glutamate dehydrogenase, which is responsible for clearing the by-products of neuron activity (44)] and the abnormal spindle-like microcephaly-associated (*ASPM*) gene and microcephalin, which are implicated in brain growth (45).

Each of these has been seen by their respective protagonists as the holy grail for understanding both social cognition generally, and, in particular, for explaining the differences between humans, apes, and monkeys (43, 46). There is no question that these are individually important and novel discoveries, and they undoubtedly all play a role in the nature of sociality. However, there is a great deal more to how and why humans are different from other apes, or why apes are different from monkeys. We will need better studies of cognition and behavior to answer these questions. More important, perhaps, is one key point: Species differences in a handful of very small

neuronal components do not explain the apparent need for massive species differences in total brain size. Most of these studies fall into the same trap as the developmental explanations for brain size did in the 1980s: They mistake mechanistic constraints for evolutionary function. It is unclear why this point continues to be ignored, but we will still have a lot of explaining to do about volumetric differences in brains.

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REVIEW

Social Components of Fitness in Primate Groups

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There is much interest in the evolutionary forces that favored the evolution of large brains in the primate order. The social brain hypothesis posits that selection has favored larger brains and more complex cognitive capacities as a means to cope with the challenges of social life. The hypothesis is supported by evidence that shows that group size is linked to various measures of brain size. But it has not been clear how cognitive complexity confers fitness advantages on individuals. Research in the field and laboratory shows that sophisticated social cognition underlies social behavior in primate groups. Moreover, a growing body of evidence suggests that the quality of social relationships has measurable fitness consequences for individuals.

Life in primate groups rivals the best television soap opera—the weak are often exploited by the powerful; strong alliances and lasting bonds are formed; dynasties are established, but are occasionally toppled; and not all of your favorite characters survive

the season. Ecological constraints generate the dramatic tension, and natural selection crafts the plot. The complicated storylines reflect the fact that primates have evolved large brains, sophisticated social cognition, and complex social relationships (Fig. 1). There has been consider-

able discussion of the selective pressures that favor the evolution of large brains in social species (1–4), but it has not been clear how large brains, social cognition, and social relationships are translated into fitness advantages for individuals. New evidence indicates that the competitive success and reproductive performance of individuals in primate groups is affected by the nature and quality of the relationships that they form. These data enable us to tie together what we have learned from comparative analyses of brain morphology, experimental studies of social cognition, and naturalistic observations of the structure of social relationships in primate groups.

What the Social Brain Knows

The capacity to develop complex social relationships may be an important benefit derived from having a “social brain.” According to the social

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