

Social Brain: Evolution

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Explaining Brain Evolution

Although neuroscientists do not often consider the evolutionary history of the brain, understanding how and why brains have evolved may help explain why they have come to have the structure they do. Vertebrate species, for example, vary enormously in both absolute brain size and brain size relative to body size, but some species (notably primates) have disproportionately large brains. Why should that be? Why do all mammals not have primate-like brains? A second issue is that brain researchers have conventionally assumed that the brain's main function is to acquire and process information about the environment, usually information directly relevant to the business of survival (i.e., finding food and avoiding predators). While obviously broadly correct, this view contains an implicit assumption that may be less defensible: the assumption that 'environment' here means the physical environment. Of course, a great deal of brain activity is about the physical environment, and, in the final analysis, it is the physical properties of the environment that constitute all perceptual inputs.

However, for more advanced vertebrates (birds and mammals), and in particular the more intensely social of these species, the environmental behavior that needs to be processed by the brain is that of the 'social' world. In the limiting case, the social world is a virtual world of behavior, the nature of which is understood and manipulated only in the animal's mind. Because the dynamic complexities of this virtual social world vastly exceed the complexities of the physical world, it is inevitably much harder to understand. Hence, intensely social species (such as primates) have brains that are specialized for dealing with this aspect of their world.

The emphasis on primates in the early literature on comparative brain evolution led to a natural focus on neocortex volume. The scaling relationships among mammalian brain units are such that neocortex volume increases much faster than that of all other parts of the brain, and especially among the primates. Although the neocortex accounts for as little as 10% of total brain volume in some of the more primitive insectivores and at most ~40% in nonprimate mammals, it accounts for a minimum of 50% in primates and rises to as high as 80% in humans. Thus, while the neocortex may be viewed as a mammalian invention,

large neocortices are clearly a primate speciality – so much so, in fact, that when one asks why primates have big brains, one is really in effect asking why they have big neocortices.

In the following sections, the selective advantages of large brains are first discussed, in order to identify why large brains have evolved in various animal lineages. Then the role that cognition plays in these processes is considered. Finally, the question of whether these forms of social cognition relate to specific brain structures is briefly explored.

Theories for the Evolution of Large Brains

We might expect large-bodied species to have large brains simply because they have larger muscle masses to coordinate if they are to survive effectively. However, it has long been recognized that some groups of species (e.g., primates) have unusually large brains for their body size compared to all other groups of vertebrates. Why this should remain so is unclear, although it has been generally assumed that it probably has something to do with the ecology of these species.

Initial Explanations

Initial attention was drawn to the fact that, within many mammalian taxa, species with larger brains have larger territories, or have diets that are more difficult to locate or process (e.g., diets of ephemeral fruits as opposed to more widely available leaves, or of invertebrates that have to be extracted from hiding places). Others have pointed to correlations with altriciality (giving birth to babies that are not mature enough at birth to move and forage for themselves) and the scaling of maternal energy demands, and have argued that it was spare maternal energy capacity that made large brains possible. By the late 1980s, however, this assumption began to be questioned: it eventually became clear that the kinds of ecological tasks faced by primates do not differ much from those faced by other species. This realization begged the question as to why primates should need a substantially larger brain (in effect, more computing power) to solve the same foraging problems as, say, cows. The social brain hypothesis was proposed as an explanation.

The initial proposal, known as the 'Machiavellian intelligence hypothesis,' was intended to explain why primates had larger brains for body size than all other species. It was suggested that this might have something to do with the fact that primates live in unusually complex social systems. Primate sociality is characterized by kinds of behaviors (for example,

tactical deception, the formation of coalitions and alliances long before they are actually needed) that are rare or entirely absent in nonprimate species. This proposal was later renamed the ‘social brain hypothesis’ (or ‘social intelligence hypothesis’) in order to avoid unnecessary and unintended implications of sociopolitical scheming and to focus attention more closely on the positive socially integrating aspects that really underpin primate sociality.

Asking the Right Questions

An important consideration at the outset is to appreciate that there is an important distinction between functional hypotheses (those that provide a reason why large brains might be selected for) and explanations that are essentially about constraints. Most developmental hypotheses fall into the latter category: they identify trajectories along which brain evolution is forced to run, or system limitations that have to be overcome. Examples of the first include the fact that the way brain tissue is laid down necessarily results in unavoidable scaling of all brain parts: if such scaling is very tight, then it may result in all parts of the brain enlarging proportionately when evolution imposes selection on just one component. This might mean that in order to evolve more capacity in some key brain component, it is necessary to evolve everything on a larger scale. Examples of the second kind of limitation would be energetic constraints that limit brain growth: some diets may not provide sufficient surplus energy that can be channeled into brain growth. Consequently, species that need to evolve a larger brain may only be able to do so if they first change diet in order to bypass the energetic constraint.

While these kinds of developmental hypotheses are perfectly legitimate and tell us something about how large brains are evolved, they do not specify why they should evolve. Given that brain tissue is among the most ‘expensive’ in the body (the so-called expensive tissue hypothesis), to merely show that evolutionary change in a particular direction is possible is not enough. The costs of evolving (and indeed growing) a large brain are such that they provide an extremely steep gradient, up which selection has to push the organism. In the absence of any selective benefit (or advantage), the costs impose strong negative selection that will constantly favor a reduction in size (or, at best, a stable state). Some real advantage of having a large brain is needed to counteract that natural stabilizing effect.

Hypotheses for Brain Evolution

In considering likely selective factors that have been responsible for driving increases in brain size, we are

left with two main contenders that can broadly be defined as ecological theories and social theories. Ecological hypotheses argue for a focus on foraging decisions (how to extract nutrients from the environment, how to find one’s way about, etc.). In contrast, the social hypotheses argue that the computational load is created by the demands of tracking social relationships and calculating the pros and cons of alternative social actions.

In both cases, of course, the fundamental issue is the brain’s problem-solving capabilities, but the focus of the problem and the mode of solution are different in each case. However, it is worth emphasizing that, either way, the root issue is essentially ecological: all animals have to overcome problems of day-to-day survival if they are to contribute offspring to the next generation (the root of all evolutionary processes). The difference lies in how this is done, and which particular computational demand imposes the highest cognitive load. Ecological hypotheses assume that the basis of an animal’s decision-making in this respect is explicitly trial-and-error learning on an individual basis; the social hypotheses assume that the ecological problems are solved cooperatively (and that the limiting cognitive demand is created by the need to coordinate one’s behavior with that of others in some way).

One way to test between these competing hypotheses is to correlate some measure of relative brain size with one or more behavioral indices that represent the hypothesis of interest. Relevant indices that have been used include the amount of fruit in the diet (representing the claim that the cognitive constraint lies in finding and monitoring high-quality food sources such as fruiting trees), the style of extractive foraging (whether or not food items are extracted from some physical matrix, such as a pod, or dug out of the ground, i.e., an index of complex food-processing decisions), day journey length and territory size (indices of mental mapping capacities), and social group size (a simple index of social complexity). When these indices have been correlated with indices of relative brain size, only group size is correlated with brain size (and specifically with neocortex size) (see [Figure 1](#)).

More recently, a number of new analyses have been undertaken that use new and more powerful statistical methods that allow the multivariate influences of a wider range of variables to be taken into account simultaneously. These have been able to show that, while other strictly ecological variables (notably, diet, diurnality, and foraging strata) play a role in brain evolution, sociality and/or social group size remain the strongest predictors of brain/neocortex volume in primates. In addition, the scope of the social brain

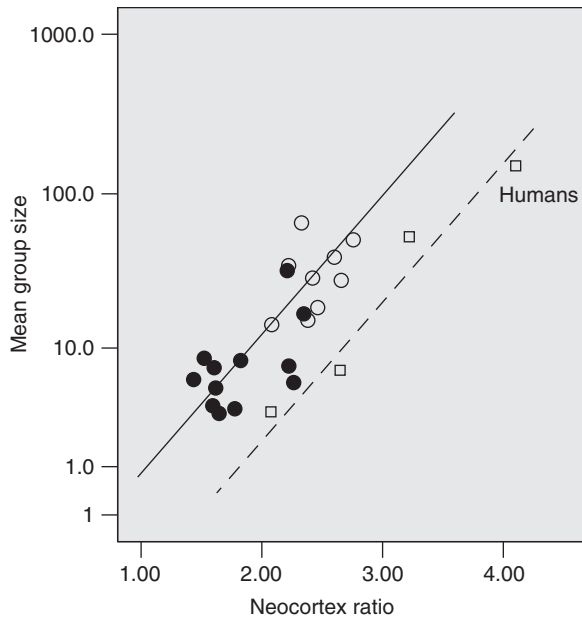


Figure 1 \log_{10} Mean social group size for different primate species plotted against relative neocortex volume (indexed as neocortex volume divided by the rest of the brain, so as to remove scaling effects due to body and brain size). Solid symbols are New World monkeys; open circles are Old World monkeys; squares are apes. Note that the apes lie on a separate grade to the monkeys: they seem to require more computing power to handle groups of a particular size than monkeys do, suggesting that their social life is cognitively more complex.

hypothesis has now been convincingly extended to other mammalian orders, including carnivores, ungulates, whales, and bats, and even to birds. In all these cases, brain size is larger relative to body size in more social species than in relatively asocial species. However, there appears to be an important distinction between the primates and all other species in the way this process works. While the main effect of this relationship in primates is a quantitative effect with group size, in all other species the effect shows up most clearly as either a contrast between social and asocial species (those that live alone, except during the mating season) or a strong effect of monogamy (monogamous species have larger brains than do those living in other mating systems). The same tendency for monogamous (i.e., pairbonded) species to have disproportionately large brains is still present in primates, but it is much overshadowed by the strong quantitative group size effect. The implications of this are explored in the following sections.

In summary, the social brain hypothesis has proved to be an extremely robust explanation for the evolution of brain (but especially neocortex) size in primates, and more generally for the evolution of brain size in mammals as a whole. It has proved to be more

successful in explaining the pattern of brain size evolution than have any of the alternative ecological hypotheses.

Social Complexity

Although the social brain hypothesis has been successfully tested using simple demographic indices like social group size or differences in mating system, its real focus lies in the subtleties of behavior. The argument is that group size is ultimately limited by the animals' abilities to maintain coherent social relationships with other individuals. Group size is thus an emergent property of animals' abilities to manage their social relationships.

This has been borne out by evidence that a number of indices of behavioral complexity also correlate with relative brain size in primates. These have included the use of coalitions, the size of alliances (indexed as grooming cliques), the frequency of tactical deception (behavior that misleads another individual), and the use of subtle social tactics that allow low-ranking males to undermine the dominant males' monopolization of matings. The fact that monogamous pairbonding (and especially lifelong pairbonding) is particularly strongly associated with large brain size across three major mammalian orders (primates, carnivores, and ungulates) likewise emphasizes the importance of social complexity, since pairbonded social systems are only possible if mates have the sociocognitive skills to negotiate a relationship in which each individual's needs are properly integrated into an effective partnership. This is most obvious, perhaps, in birds, where the pair has to coordinate and schedule two major activities: sitting on the nest (to keep eggs or fledglings warm and protected) and foraging.

The significance of social complexity as opposed merely to sociality, at least in primates, is given further emphasis by the fact that development can be shown to play an important role. While it has long been known that total brain size correlates with the level of parental investment (as indexed, for example, by the duration of pregnancy and lactation), neocortex volume correlates best with the period between weaning and puberty (i.e., the main period of socialization before the animal finally joins the adult world). This suggests that growing a big brain depends on how long the mother can afford to invest in direct parental care, but having a socially complex brain (and this really means neocortex) depends on the time you can afford to invest in socialization (in effect, the equivalent of the software programming). Further evidence is provided by the fact that, in primates, neocortex size also correlates with the proportion of all play that

is social (as opposed to instrumental or solitary): most social play takes place during this main period of socialization between weaning and puberty.

Thus, although brain size is the central issue in the social brain hypothesis, it is important to appreciate that the situation is rather different from that in the case of more conventional brain systems. A distinction needs to be drawn between what we might think of as first-order processing systems (those in which sensory inputs are analyzed for their intrinsic patterns) and those which involve secondary or even tertiary analyses of these inputs (e.g., those in which meaning is attached to the sensory patterns). While sensory processing mechanisms function more or less efficiently from the moment the animal engages with the world, the upstream neural systems responsible for adding the layers of social meaning (and which thus constitute the heart of the social brain) seem to require extensive tuning before they can operate at full capacity. That tuning presumably occurs in the social environment provided during development.

The Nature of Social Cognition

We do not have a clear idea of how cognition interfaces between the neural systems of the brain and the observable behavior of the animals in the social domain. However, there is general agreement that, at least in primates, it involves specialized processes that are collectively but loosely termed ‘social cognition.’ In humans, these are identified with the cognitive mechanism known as ‘theory of mind’ or ‘mentalizing’ (the ability to understand the minds of other individuals). Although the exact nature of this phenomenon is still a subject of debate, it provides at least a useful way of thinking about the general cognitive demands of sociality.

Theory of mind refers to the capacity to mentally represent another individual’s mind state: “I *believe* that you *suppose* . . .” This is generally understood to be equivalent to what philosophers of mind refer to as second-order intentionality, where intentionality refers to the capacity to use words that involve the ‘intentional stance’ (in other words, the ability to reflect on one’s intentions, or more generally one’s beliefs about the world). In principle, intentionality forms a reflexive hierarchy that is infinite: “I *believe* that you *suppose* that I *intend* that you *want* me to *understand* . . .” Theory of mind is generally held to be acquired by children at around age 4 years. Prior to that, children, in common with all nonhuman animals, have only first-order intentionality: in effect, they understand their own minds, but not those of other individuals. The only exception to this is the chimpanzee (and possibly other great apes), for whom

there is some (albeit weak) evidence for second-order intentionality. In contrast, normal adult humans are able to cope with fifth-order intentionality. These additional levels of intentionality appear to be acquired sequentially by the early teenage years.

Although we know quite a lot about theory of mind (but rather less about the higher levels of intentionality), in fact we do not really know what it actually is. There are two views on this: one views theory of mind as a specialized cognitive module; the other views it as simply a product of more conventional executive functions (memory, causal reasoning, etc.). An alternative view is that theory of mind is an emergent property of a number of other higher order cognitive abilities, including causal reasoning, analogical reasoning, the time frame over which consequences of actions can be forecast, the ability to compare two behavioral trajectories through time, etc. These might be viewed as ‘middle-range’ cognitive modules that intervene between the more conventional Fodorian modules (those associated with basic percept processing) and the higher order inferential processes associated with social cognition.

In effect, theory of mind is what ‘pops’ out when an individual can do all of these on a large-enough scale and focus them sufficiently onto a single problem. In other words, it is an emergent property of cognitive mechanisms that are both general and essential for everyday life. This being so, on a simple information-processing model, we might expect the ability to engage these middle-range processing capacities to be a function of brain size. Presumably, the capacity to engage in higher levels of intentionality beyond theory of mind (level 2) is simply a reflection of a correspondingly greater computational capacity.

Cognition and the Brain

This brings us to the last issue we need to consider, namely exactly how these higher order aspects of social cognition relate to the brain. There appear to be two possible positions on this. One is that several decades of research in neuroscience is enough to make it clear that the interconnectedness of the brain is of such an order that it does not make sense to consider the brain as modularized in any naïve sense: it functions as an integrated whole, in which processing capacities of different kinds are called up from different cortical and subcortical regions. The alternative view is that the specialized cognitive functions identified with theory of mind and social cognition can be equated with particular brain regions (specifically in the neocortex).

While it may be true that brain function does commonly involve activity in many parts of the brain that

are physically distant from each other, nonetheless there is convincing evidence that these higher-level skills are associated with specific neocortical regions, and specifically with the frontal lobe (an area of the brain that has proved to be singularly resistant to attempts to partition it into functional subunits). There is considerable clinical evidence, from the famous case of Phineas Gage in the 1890s onwards, that stroke or physical injury to the frontal lobes is particularly likely to disrupt social skills (and only social skills). However, several other sources of data also suggest that the frontal lobe of the neocortex plays a critical role in social cognition.

First, a detailed analysis of data for primates shows that when all other brain components are held constant, only neocortex size correlates with social group size; no other brain unit has any association with group size. Indeed, the correlation between neocortex volume and social group size improves measurably if the primary visual cortex is removed, and improves still further if only the frontal lobe volume is considered. In other words, the more one focuses on the frontal lobe, the better the relationship seems to be. Second, such differences as there are in mentalizing capacity between primate species (essentially first-order intentionality in monkeys, second order in apes, and fifth order in adult humans) are linearly related to frontal lobe volume, but not to any other part of the brain. Finally, neuroimaging studies have emphasized a particularly important role for frontal lobe units in social cognitive tasks (even though units elsewhere in the parietal and temporal lobes may also be involved).

One reason why the more occipital areas of the brain may not play a central role is that, as the principal visual areas, they are mainly concerned with primary and secondary visual processing, and the computational demands for this are largely dependent on the sensory input from the retina. Indeed, there is a near linear relationship in primates between orbit volume (and hence retinal area) and volumes of the successive segments of the visual pathway (optic nerve, lateral geniculate nucleus, and primary visual cortex in the occipital lobe). This is, in part at least, a consequence of the fact that the size of the retina is the rate-limiting factor in visual acuity, and there is little point in having a cortical visual processing capacity that is more powerful computationally than its input. Indeed, this seems to be a general principle in brain system organization. Hence, with orbit size relatively constant across primate species, any increases in brain volume are mainly associated with more frontal brain units.

Indeed, the brain (and neocortex in particular) is known to both evolve and develop from back (occipital

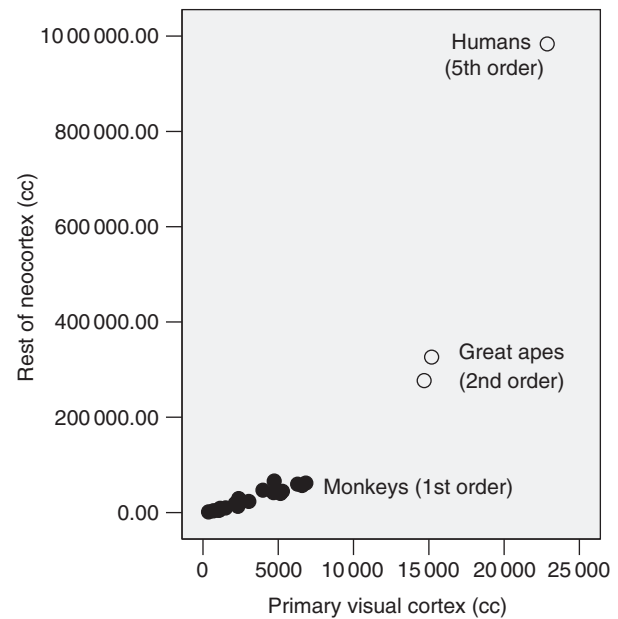


Figure 2 Neocortex volume excluding the primary visual area plotted against the primary visual area for different monkey and ape species. Solid symbols, monkeys; open symbols, apes. The maximum achievable level of mentalizing (intentionality order) is indicated beside each major group, and suggests that brains of the size seen in the great ape mark a critical juncture at which spare neural capacity in the more frontal units of the brain suddenly becomes available, thus allowing higher orders of mentalizing to develop.

lobe) to front, so that increases in brain volume are largely associated with increases in frontal lobe volume. Plotting 'spare' neural volume over and above that predicted by primary visual area (Figure 2) suggests that the volume of spare capacity (most of which is in the frontal lobe and thus supports executive function) starts to increase disproportionately at the brain size of great apes (i.e., just at the point where we have the first evidence for second-order intentionality) and is massive in modern humans (with their fifth-order capacities).

See also: Brain Connectivity and Brain Size; Brain Development: The Generation of Large Brains; Brain Evolution: Developmental Constraints and Relative Developmental Growth; Brain Scaling Laws; Evolution of Vertebrate Brains; Neuroendocrinology of Social/Affiliative Behavior; Social Interaction; Social Interaction Effects on Reward and Cognitive Abilities in Monkeys.

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