Primate cognition: from ‘what now?’ to ‘what if?’

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The ‘social brain’ hypothesis has had a major impact on the study of comparative cognition. However, despite a strong sense, gained from both experimental and observational work, that monkeys and apes differ from each other, we are still no closer to understanding exactly how they differ. We hypothesize that the dispersed social systems characteristic of ape societies explains why monkeys and apes should differ cognitively. The increased cognitive control and analogical reasoning ability needed to cope with life in dispersed societies also suggests a possible route for human cognitive evolution. This hypothesis is supported by behavioural and neurobiological data, but we need more of both if we are to fully understand how our primate cousins see the world.

Primates have unusually large brains for body size. It is now widely recognized that this is mainly associated with their distinctive social skills (the ‘Machiavellian intelligence’ [1] or ‘social brain’ hypothesis [2,3]). Within the primate array, however, there are significant differences in competence – most strikingly between monkeys and apes – both in general cognitive abilities and, more importantly, in social behaviour and sociocognitive skills. These contrasts seem to parallel differences between species in key aspects of brain evolution [4–6].

However, despite extensive psychological experimentation, the exact nature of the cognitive differences between monkeys and apes are unclear [7], and the degree to which apes are capable of any form of metarepresentational thought (whether socially-based or not) remains contentious [8,9]. We suggest that this is because the tests have not been exhaustive and/or the right kinds of tests have not been performed. The latter could be because much of the work on social cognition has been anthropocentric, seeking to discover which human cognitive characteristics are shared by our simian cousins [10]. The same is true from a neurobiological perspective, where the use of monkeys as a model species has meant, again, that similarities between non-human primates and humans have been highlighted at the expense of distinctive differences. It is only recently that researchers have begun to probe for neurobiological differences that might be linked to the apparently unique features of human cognition, such as language and metacognition [11].

Here, we present a new hypothesis to explain the differences between monkeys and apes, based on an understanding of the ecological constraints under which these animals operate. Specifically, we argue that the dispersed social systems (‘fission–fusion’ societies) in which most (if not all) of the hominoids (apes and humans) live can be viewed as cognitively more demanding social ‘market places’ than monkey groups. The demands of navigating a more complex social landscape thus constituted a unique selection pressure among the ancestral apes for increased brain size and cognitive abilities. This ecologically-valid approach will, we hope, enable researchers to uncover the cognitive differences that have, so far, been concealed.

The social market place

To date, the social brain hypothesis has focused on a general notion of social complexity (often indexed by group size) as a driving force in brain evolution [3] and has not attempted to explain how the particular characteristics of species’ social structure are related to cognitive capacity. However, recent empirical work on non-human primates [12–14], along with theoretical speculations on humans [15], suggests that applying a ‘biological markets’ [16] framework to studies of primate sociality might help point the way to more informative experimental studies of monkey and ape cognition. The theory of biological markets views animals as traders engaged in a mutually beneficial exchange of commodities. Individuals within a biological market attempt to maximize ‘profit’ (in terms of fitness) by selecting social partners that offer the best value, with an exchange rate set by the supply and demand of the commodity in question.

Unlike standard optimality models of decision making, market models are inherently dynamic, recognizing that individuals’ decisions vary across time according to local circumstance. They are perfect for the analysis of social decision-making because the social world is also inherently dynamic: each individual has its own particular set of desires and goals that might not coincide with those of others and decisions therefore reflect an ongoing process of negotiation.

Studies of baboons (Papio hamadryas ursinus) [12–13] and chimpanzees (Pan troglodytes) [14] have shown that animals trade grooming as a ‘service’, either for its own
utilitarian value or for its value equivalent; moreover, true market effects can be found, with the duration of grooming (the ‘price paid’) varying in relation to the supply of particular commodities [13]. Viewing primate groups as market places allows us to refine the social brain hypothesis because we can identify the key differences between ape and monkey market places and thus predict consequent differences in cognitive skills.

A market for brain power
In primate market places, individuals must track the price of commodities and respond flexibly to changes in supply and demand. This agrees with the ‘Machiavellian intelligence’ hypothesis, in that sociality is assumed to drive brain evolution. It differs, however, by assuming that animals have not been selected to cope with increasingly elaborate strategies and counter-strategies, the goals of which are to ‘outwit’ the competition. Instead, it assumes that the evolution of brain size and structure have been driven by a need to track fluctuations in commodity value.

Monitoring the market place is intrinsically complex because the value of a particular partner is contingent on the value of others. Each of these values can shift with changes in reproductive state, health, dominance and ongoing social behaviour. Those who are good value today might not be so tomorrow. This constant state of flux means that keeping tabs on the social market is very different from the other kinds of contingent monitoring that primates must do, such as tracking fluctuations in fruit availability [17]. Fruits, unlike conspecifics, do not make decisions of their own in response to primate behaviour. This inherent contingency in primate market places thus selects for a ‘knowledge-based’ [18], rather than strictly cue-based, understanding of others, as evidence from monkeys and, to an even greater degree, apes has shown [18]. Nevertheless, there remains a cognitive difference between monkeys and apes that, although poorly characterized, is apparent when comparing their performance on psychological tests [7,19–20]. It is also apparent that there are distinct grades within the brain data that point specifically to increased cognitive powers among the apes [3,6,21] (Figure 1). We suggest that these emerged because of a key difference in the market places of these two taxonomic groups.

Whereas monkeys are all highly gregarious and live in cohesive groups in which individuals encounter every member of their group every day, the apes – in particular, the chimpanzee and orang-utan (Pongo pygmaeus) – live in more fragmented societies as a result of food competition, which forces females to forage in small parties or alone [22]. The apparent exceptions to this – group-living gorillas (Gorilla gorilla) and fission–fusion spider monkeys (Ateles spp.) – are less convincing than might seem at first sight. Among gorillas, group living might be a relative recent adaptation in response to infanticide by adult males [23]. More importantly, our conception of gorilla society has been determined entirely by a single (ecologically rather atypical) population (the Virunga mountain gorillas); a fission–fusion pattern of sociality has been reported from western lowland gorilla populations [24] and may in fact be more typical of gorillas as a whole. By contrast, the nature of spider monkey fission–fusion is not well studied and could differ from apes in important ways. If, however, their behaviour is truly ape-like, then we have an ideal test case: we would predict that they manifest ape-like cognitive abilities – something that is, perhaps, hinted at by the fact that they are one of the most encephalized of the South American monkeys.

In fission–fusion societies, individuals see each other only at infrequent intervals, often weeks apart, yet each recognizes the members of its community and is capable of maintaining long-standing relationships. In such systems, individuals must be able to represent mentally individuals that are not present and to retain and manipulate information about them for substantial periods of time, whereas there is no such pressure for these abilities to evolve in spatially and temporally stable monkey groups where animals are only out of view for at most a few hours. The computational load required to monitor and track changes in a dispersed ape market place is therefore significantly greater than when members of a group see each other every day [6]. A salient point to note in this context is that humans also live in dispersed societies based on fission–fusion dynamics [25].

Monitoring space and time
More importantly, in terms of monitoring the state of their social market place, animals need to recognize that the absence of a particular individual can affect the relative value of those that are present, and can reliably predict the occurrence of certain behaviours in others in just the same way that the presence of that individual does. They also need to be able to track and update any changes observed in the interactions of others when particular animals come into contact after a period of absence. Although all anthropoid primates are capable of tracking ‘third-party relations’ (relationships between two other animals without reference to self) [7], the ability to generate a causal understanding of such behavioural interactions in the absence of certain individuals would seem to be much more
demanding cognitively. Thus, the key to social survival in dispersed societies is the ability to work with a social world that is partially virtual, rather than purely physically instantiated. The fact that chimpanzees are apparently able to represent the relative spatial locations of stone tools (hammer stones and anvils) and to use this information in a flexible manner [26] supports the notion for a similar capacity in the social domain. Intriguingly, the finding that scrub jays also show such abilities [27] suggests that an episodic-like memory (the ability to represent ‘what, where, when and who’) is a precursor to more highly developed aspects of cognition, rather than the outcome of these processes.

Analogical abilities

Boroditsky has argued that, in humans, the sense of time emerges via a metaphorical analogy from a sense of space [28]. This suggestion provides the basis for a promising explanation for cognitive evolution among the hominoids: a sense of space could, with sufficient additional cognitive control, be used to develop an extended sense of time, thus enabling animals to predict future states of the market place, as well as track current changes, in a very effective way. If the ability to engage in analogical reasoning scaffolded this development, as Boroditsky suggests [28], then a plausible suggestion would be that, combined with the ability to reflect on a virtual world, an understanding of future time would have led to the emergence of an ability to sequence social events temporally into causal chains, which such an ability was selected.

Such a stance can perhaps give some insight into how apes and humans differ from each other as well. Given further increases in brain size within the hominid line (whether socially-driven or not), an initial ability to represent the self and others in different spatio-temporal locations could have scaffolded the development of higher metacognitive skills, leading eventually to full-blown ‘theory of mind’ skills in modern humans [29–30], we can add an important new dimension by identifying the likely ecological context in which such an ability was selected.

In humans, many of our more advanced cognitive skills are associated with improved executive function [7] and the expansion of the frontal lobes [39], particularly the lateral pre-frontal area. Miller and Cohen [40] have argued that this is related to the need for greater ‘cognitive control’ – the ability to take charge of one’s actions and direct them towards future, unseen goals. Their model thus fits beautifully with our ideas concerning the selection pressures acting on hominoid brains. They argue that the PFC effectively constructs a map of the neural pathways needed to solve a task, thereby allowing an organism to escape reality and gain greater control of its actions by forming abstract representations that are not linked to specific associations, but which correspond to overarching principles and concepts. As both the frontal lobes [39] and the prefrontal cortex (41,42) of the macaque (Macaca sp.) are significantly smaller than those of humans and apes (in the case of prefrontal cortex, 11% of total cortical volume in macaque, compared with 17% and 36% for chimpanzees and humans, respectively [41]), it is likely that monkeys will be more limited in this respect than both apes and humans (and by the same token, that apes will be more limited than humans) [6]. However, the PFC is not the only element crucial for achieving cognitive control. Allocation of control might also depend on the anterior cingulate cortex (ACC), an area variously associated with error detection, response selection and conflict monitoring [43–45]. By detecting conflict signals, the ACC is able to signal that additional control needs to be allocated to a task. It has also been suggested that the upgrading of the ACC would have enabled the construction of a ‘troop in the head’ because it is also linked to generating a sense of self in relation to others [46]. In this respect, it is intriguing that spindle cells, a class of large projection neurons found principally in the ACC region, are found only in apes and humans, not monkeys [47]. Allman et al. [48] have speculated that these are involved in coordinating widely distributed neural activity involving emotion and cognition, again fitting well with our speculations on the need for greater attention-to-action and cognitive control within a dispersed ape market place. The role of cerebellar–neocortical circuits in coordinating cognitive functioning might also be crucial in this respect [49]; recent work has identified an expansion of the cerebellum across the primate order, suggesting that evolution has acted on distributed systems of functionally related components in just this way [50].

**Box 1. A neurological basis for social cognition**

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The significant experimental evidence in support of its basic elements [35–37] gives us some confidence in developing our hypothesis that the difference between monkeys and apes stems from the time frame over which they can monitor their social market places. However, owing to the gap in our knowledge of the neurobiological differences between monkeys and apes, we can be less sure about how these cognitive differences map onto brain structure and function. Although the functions of those brain areas that show expansion across the primates support our proposal, most of these data are from humans (Box 1). However, we hope that a new perspective will encourage both cognitive psychologists and neurobiologists to probe more deeply into how monkey and ape brains differ from each other, both structurally and functionally.

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