

Review

The social nature of primate cognition

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The hypothesis that the enlarged brain size of the primates was selected for by social, rather than purely ecological, factors has been strongly influential in studies of primate cognition and behaviour over the past two decades. However, the Machiavellian intelligence hypothesis, also known as the social brain hypothesis, tends to emphasize certain traits and behaviours, like exploitation and deception, at the expense of others, such as tolerance and behavioural coordination, and therefore presents only one view of how social life may shape cognition. This review outlines work from other relevant disciplines, including evolutionary economics, cognitive science and neurophysiology, to illustrate how these can be used to build a more general theoretical framework, incorporating notions of embodied and distributed cognition, in which to situate questions concerning the evolution of primate social cognition.

Keywords: primate; social brain; embodied cognition; distributed cognition; mirror neurons

1. INTRODUCTION

It is well known that, compared to other mammals of equivalent size, primates have brains that are approximately twice as large as expected (Passingham 1981). From the 1950s onwards, a number of researchers have argued that this increase in brain size is causally linked to another distinctive feature of the primates: their intense sociality (Chance & Mead 1953; Jolly 1966; Humphrey 1976). These ideas were brought together most prominently by Byrne & Whiten (1988) in the form of the ‘Machiavellian intelligence’ hypothesis. They proposed that, as a consequence of living in permanent social groups with local competition for scarce resources, the pressure was on for animals to evolve an ability to ‘out-wit’ other group members. This would thereby alleviate the negative effects of competition on reproductive success and, in turn, trigger a cascade of increasingly elaborate cognitive counter-strategies.

Brothers (1990), focussing on particular structures within the brain, suggested similarly that primates possess a ‘social brain’, while Dunbar (1992, 1995, 1998) demonstrated a relationship between primate group size and neocortex size (the most recently evolved part of the primate brain, and the area that has undergone the greatest expansion compared to other mammals). This relationship was thought to reflect the cognitive demands of both tracking a complex web of relationships through time and the forming of coalitions and alliances. Such alliances, as with the notion of more overtly ‘Machiavellian’ intelligence, were construed as long-term strategic responses, necessarily cognitively derived, designed to alleviate the negative consequences of group-living. Studies of reconciliation (peaceful post-conflict contact between former opponents) also served to emphasize the importance to primates of the long-term value of their relationships (de Waal & van Roosmalen 1979; Aureli & de Waal 2000).

Dunbar’s argument also dovetailed neatly both with Seyfarth’s (1977) influential model, in which grooming was related to competition over access to valuable female coalition partners, as well as with work on the ecology of social relationships (van Schaik 1989; Sterck *et al.* 1997), which hypothesized that the nature of local competition determined the nature of grooming bonds and coalitionary behaviour. In all cases, grooming was taken to function as the ‘social glue’ that facilitated coalition formation between individuals (Dunbar 1988). The task of juggling one’s own grooming and coalitionary relationships, while simultaneously tracking everyone else’s, was viewed as a strong social selection pressure on cognitive capacities and, hence, brain size (Dunbar 1998; Kudo & Dunbar 2001).

The ‘Social Brain’ hypothesis (Dunbar 1998), as it became known, is therefore a powerful and persuasive argument. It builds on the foundations of the cognitive revolution in psychology by presenting a picture of primates as biologically prepared for forms of social engagement that require the mental representation of abstract concepts, like social bonds and alliances, in order to negotiate the social landscape. It also receives substantial support from data on the neurobiological correlates of social life (e.g. Brothers 1990; Perrett *et al.* 1990; Dunbar 1995, 1998; Barton 1996, 1998; Keverne *et al.* 1996; Barton & Dunbar 1997; Pawlowski *et al.* 1998; Byrne & Corp 2004).

Nevertheless, despite its congenial synthesis of behavioural ecology and neuroanatomy, the Social Brain hypothesis presents a particular view of primate sociality and cognition, which is one that bears the imprint of its origins in the Machiavellian intelligence hypothesis. Whereas this places problems of manipulation, deceit and cheat detection to the fore, recent empirical and theoretical work both suggest that cooperation, compromise, ‘trade’ and other ‘prosocial’ behaviours are important elements of

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primate, especially human, social life (de Waal 1997a,b; Barrett & Henzi 2001, 2005; Noë *et al.* 2001; Fehr & Fischbacher 2003; Hammerstein 2003; Roberts *in press*). It is also heavily oriented toward a particular model of cognition that focuses solely on internal mental representations, whereas recent work in cognitive science and neurobiology argues for a more ‘distributed’ and ‘embodied’ approach (e.g. Clark 1997; Brooks 1999; Rowlands 1999; Gallese 2001; Johnson 2001; Garbarini & Adenzato 2004; Anderson 2005). Our aim is to outline some of this new work and show how it can be incorporated into, and thus enrich, the social brain hypothesis.

2. MACHIAVELLIAN INTELLIGENCE AND THE ROOTS OF PROSOCIAL BEHAVIOUR

Despite a prominent disclaimer that not all primate cognition is characterized by deceit and underhandedness, Byrne & Whiten (1988) justified their use of the term ‘Machiavellian’ by appealing to the fact that most of the existing data were consistent with the kinds of recommendations made by Machiavelli. Even in cases involving cooperation between individuals, they argued, ‘its usual function is to out-compete rivals for personal gain’ (Preface, page vi), thus echoing Humphrey’s (1976) earlier paper, in which he suggested that there were benefits to be gained from exploiting and out-manoeuvring others. Consequently, Machiavellian/social intelligence was viewed from the outset largely as a zero-sum game in which manipulating others for personal gain was achieved at a cost to the manipulated individuals. Sociological evidence that group-mates are unwilling collaborators forced to live together to avoid predation (or infanticide), and the derived supposition that they deal with the consequences in a self-serving manner, only reinforced this view (Dunbar 1988; van Schaik 1989; van Schaik & Kappeler 1997).

While this conception of primate behaviour is accurate—competition is inevitable in a world of finite resources—it tells only half the story. For social individuals to survive, groups must be cohesive and persistent. As much of the earlier literature points out, primates have evolved adaptations that allow them to function well in a group setting. de Waal (1982, 1989, 1997a), for instance, has long championed the view that aggression is an instrument of negotiation for non-linguistic animals that, together with affiliative behaviours like grooming, enables animals to set the boundaries of their relations and thereby coexist peaceably. Animals that can negotiate an increase in social cohesion can therefore expect to be more reproductively successful than those that live in groups where more anarchic interaction reduces cohesion. Here the game is likely to be non-zero-sum.

This outcome may emerge through a process of multi-level selection (Sober & Wilson 1998) that, while remaining controversial (e.g. Cronk 1994), is receiving increased theoretical and empirical support, especially from work on human sociality (see e.g. Richerson & Boyd 2005). Roberts (*in press*) has also shown, using a modelling approach, that stable outcomes can evolve even under individual selection whenever an altruistic/cooperative animal has some interest or ‘stake’ in the welfare of the recipient of its altruistic act. Under these conditions, altruists benefit as a secondary consequence of

their own behaviour: being altruistic can therefore be in one’s own long-term best interests. Having a stake in a partner’s pay-off allows cooperation to escape the prisoner’s dilemma because the feedback effect from recipient to donor ensures that mutual cooperation results in the highest pay-off. Without a temptation to defect, the dilemma disappears. This also means that stakeholder cooperation does not require repeated interactions in order to be stable.

For there to be secondary benefits accruing from altruistic acts, individuals must be inter-dependent so that individual fitness is linked to the fitness of others. Cooperative breeders are an obvious example of such mutual dependence and work on meerkats (Clutton-Brock 2002) presents a clear empirical demonstration of ‘stakeholder cooperation’, with mutual cooperation yielding larger payoffs than cheating for individual animals (see also Grinnell *et al.* 1993 on cooperative pride defence among male lions). However, as Roberts (*in press*) points out, this condition of inter-dependence is met in many social groups, where increasing group size tends to reduce individual predation risk. Primate groups may therefore represent a prime example of the inter-dependence between individuals. This suggests that stakeholder cooperation may explain many patterns of primate social engagement, in which cooperative behaviours are favoured because they provide positive benefits for both donor and recipient, and not because they enable a more efficient exploitation of others.

Roberts’ model also provides a link to group selection models, as the stake measures the extent to which the interests of the individual coincide with the group: a perfect correspondence between the two means that selection can be seen as acting on the group as a whole. Cooperation through inter-dependence highlights the fact that one should not take it as axiomatic that cheating will always trump cooperation, and that individual strategies that are fundamentally linked to the well-being of others can emerge by standard evolutionary processes. Acknowledging that the competition inherent in social life is counter-balanced by these inter-dependencies allows us to refocus attention onto arguments concerning the positive adaptations to group-living that have sometimes been lost or overlooked with the rise of Machiavellian intelligence.

There is, moreover, another good reason to highlight such positive social adaptations here. Namely, that they may help shed light on findings from the field of evolutionary economics, where strong prosocial tendencies have been found to characterize human behaviour (Fehr & Gächter 2002; Fehr & Fischbacher 2003). In experimental economic games, individual behaviour is consistently characterized by both strong reciprocity (an economically irrational willingness to cooperate in the absence of any personal incentives) and altruistic punishment (an economically irrational desire to punish miscreants at a cost to oneself).

Some authors suggest that this behaviour is merely the maladapted by-product of past selection acting on humans living in small kin-based groups. According to this ‘Big Mistake’ hypothesis, the psychological mechanisms underlying these behaviours are not fine-tuned enough to differentiate the current and novel experimental context from the past situation to which these mechanisms are adapted (e.g. Johnson *et al.* 2002). There is also the

argument that high levels of cooperation are largely maintained by reputational concerns (Milinski *et al.* 2002; Semman *et al.* 2004, 2005). However, this does not explain why people initially cooperate when it is irrational to do so, nor why they do so in the absence of the ability to build reputation (Fehr & Henrich 2003). Others argue, therefore, that these behaviours are the adaptive products of cultural group selection, and mediated by strong emotional responses (Fehr & Henrich 2003; Richerson & Boyd 2005).

While the challenge from those engaged in reputation-based research remains to be answered, most theoretical and ethnographic evidence favours this latter explanation (Fehr & Henrich 2003; Richerson & Boyd 2005). Equally convincing evidence against the Big Mistake hypothesis is provided by the fact that non-human primates display a fine-tuned ability to differentiate among partners, despite living in small kin-based groups (Barrett *et al.* 1999; Barrett & Henzi 2002; Henzi & Barrett 2002; Silk *et al.* 2003, 2004; Richerson & Boyd 2005). It therefore seems implausible that humans should not be able to do the same (Fehr & Henrich 2003; Richerson & Boyd 2005). Even more interesting is the fact that no form of 'strong reciprocity' has been observed in any non-human primate group (Fehr & Henrich 2003).

Such data suggest that specifying more precisely the limits of prosocial (or proto-prosocial) behaviours among the living primates would allow us to disentangle the effects of cultural and natural selection still further. We would be able to refine our assessment of which cooperative mechanisms have deep ancestral roots and which are of more recent origin (Noë 2005, *in press*), and explain in more detail the role played by both positive and negative emotions in mediating social responses (Aureli & Schaffner 2002; Preston & de Waal 2002). Some work in this direction is now beginning, dealing mostly with cooperation in experimental tasks (Noë *in press*). It probes the extent to which animals are capable of coordinating their behaviour to achieve a common goal (e.g. Chalmeau & Gallo 1996; de Waal 2000; Brosnan & de Waal 2002, 2003; Hauser *et al.* 2003; see also Stevens & Hauser 2004), and how social tolerance and familiarity affect these results (Brosnan *et al.* 2005). Most recently, Flack *et al.* (2005) have probed the robustness of conflict management mechanisms arguing that the presence of animals that act as 'conflict managers' is essential for the stability of social groups through time. This focus on how animals work together, as opposed to 'out-witting' each other, is exciting and may help us understand better the continuity between our behaviour and that of other primates, as well as appreciate how strongly it differs. Understanding how, why and when behavioural coordination is achieved may also provide greater insights into the cognitive processes that underlie this capacity (see below).

3. MUNDANE, NOT MACHIAVELLIAN, INTELLIGENCE

The social intelligence hypothesis can sometimes appear circular: primates have large brains because their social lives are cognitively demanding, and their lives are cognitively demanding because they have large brains that allow them to produce more complex forms of social

behaviour. Or, as Gigerenzer (1997) put it, part of the complexity of the social environment is its 'perceived complexity', which is not a feature of the environment *per se*. Such perceived complexity cannot explain why a certain level of social intelligence is present in a species because 'the perceived complexity is itself dependent on, or even part of, social intelligence' (see also Strum *et al.* 1997).

This circularity arises partly because the Machiavellian intelligence/social brain hypothesis was initially concerned with determining the degree to which an animal required an ability to 'mind-read' (to attribute mental states, like beliefs and desires, to others) in order to engage in socially complex ways (indeed 'Are primates mind-readers?' was the title of one section in Byrne & Whiten 1988). With ideas of complex mental representation so strongly to the fore, it is not surprising that the complexity of primate social worlds became so closely linked to the level of internal mental complexity the animals themselves possessed.

The problem, however, is that while this debate persists with respect to apes (e.g. Hare *et al.* 2000, 2001; Povinelli *et al.* 2000; Povinelli & Vonk 2003; Tomasello *et al.* 2003), it is now widely accepted that monkeys show no understanding of the thoughts, beliefs and desires of others or, indeed, of their own. As Cheney & Seyfarth (1990) concluded, although monkeys have mental states, they do not know that they have them. If monkeys do not perceive their social environments as intricate webs of beliefs, desires, tactics and strategies, then what makes them complex? Is the proposition of social complexity 'empirically empty' as Gigerenzer (1997) suggested?

One way out of this 'mindreading' dilemma was, as mentioned above, to fall back on the suggestion that tracking many relationships through time, especially those among other animals ('triadic relationships': Tomasello & Call 1997), is cognitively demanding, even in the absence of mental state attribution (Cords 1997; Tomasello & Call 1997; Dunbar 1998; Kudo & Dunbar 2001). In this formulation, grooming relationships, functionally linked to coalition formation, were seen as the key to social cognition, with appropriate partners selected and cultivated (through grooming) ahead of the point at which their assistance in the pursuit of social goals was required (Harcourt & de Waal 1992). Decisions regarding who to groom, who to support and who to attack, when to engage and when to hold back were seen as complex, long-term strategic responses that had to be the product of 'mind' in some sense, as opposed to an evolved response that did not require cognitive assessment. This slippage between evolutionary versus cognitive strategies was inevitable, since the phenomenon to be explained—large brain size—required primates to be doing more with their brains than other, less well endowed taxa (Strum *et al.* 1997).

The ability of monkeys to engage in any long-term strategic planning in the cognitive sense was assumed, however, rather than explicitly tested. While monkeys can recognize triadic relations (e.g. Tomasello & Call 1997; Silk 1999; Perry *et al.* 2004) and potentially understand visual perspective in others (Flombaum & Santos 2005), it is becoming increasingly apparent that the time-frame over which they can plan is relatively short (Barrett & Henzi 2001; Roberts 2002), that their ability to engage in causal and analogical reasoning is limited (Visalberghi &

Limongelli 1994; Thompson & Oden 2000) and that they lack the ability to inhibit inappropriate social responses. Chapais (1992) observed that high-ranking juvenile macaques (*Macaca fuscata*), whose relatives had been removed from the group and who therefore lacked support, nevertheless continued to challenge subordinate animals in intact matriline, resulting in a costly loss of rank. As all these skills are essential to long-term strategic coalition behaviour, their lack suggests that monkeys may solve certain social problems through the use of simple evolved or learned 'rules of thumb' that require much less in the way of cognitive skill (Barrett & Henzi 2001; Range & Noë 2005).

Moreover, the evidence for coalition formation as a general organizing principle of group life has also been called into question (Henzi & Barrett 1999). A recent, comprehensive analysis has revealed that coalitions in wild female baboons, for example, were not tied to grooming and were extremely rare. When they did occur they were opportunistic interactions where the benefits to both parties were immediate, rather than a result of the reciprocal trading of favours over time (Silk *et al.* 2004; see also Stevens & Hauser 2004 for limitations on primate cognitive abilities involved in reciprocity).

Indeed, as such data accumulate, they suggest that monkeys have more short-term concerns than Machiavellian alliance formation, and that they use grooming to achieve immediate goals within a social 'market-place' of trading (Barrett & Henzi 2001, 2005; Noë 2005). Such mundane 'quotidian cognition' is seen in the way in which females select the most appropriate exchange partners (Henzi *et al.* 2003; Chapais 2005), exchange grooming for its own benefits (Barrett *et al.* 1999; Leinfelder *et al.* 2001; Payne *et al.* 2003; Manson *et al.* 2004; but see Schino *et al.* 2003), for food (Stammach 1988; de Waal 1997b) and to gain access to other females' infants ('baby trading': Muroyama 1994; Henzi & Barrett 2002). Data on reconciliation also suggest that, instead of subserving long-term relationships, it functions to reduce aggression in the short-term (Silk 1996, 2002; but see Cords & Aureli 1996).

It should be noted that we do not deny the importance of coalitions in some arenas, such as achieving rank among immatures (Henzi & Barrett 1999), or that they may involve tactical responses by animals that require complex third-party knowledge (e.g. Silk 1999; Perry *et al.* 2004; but see Range & Noë 2005). Nor are we suggesting that all facets of social behaviour are expedient short-term solutions. Group-living itself is clearly a long-term solution to the problem of predation, and enduring kinship bonds are also notable in many primate species (although we would argue that the mechanisms supporting these are based on evolved rules of thumb). Our only point is that the manner in which Machiavellian alliance formation was initially conceived assumed a suite of cognitive skills that monkeys, at least, do not appear to possess.

4. QUOTIDIAN COGNITION AND EXPEDIENCE

It seems that it is not what monkeys are that is more complex (in terms of mindreading abilities), nor what they do that is necessarily more complex (in terms of strategic planning). It is, rather, the number and variety of ways in which they achieve their short-term goals that differentiates

them from other mammals: they can achieve the same goal in a number of different ways (aggression can be avoided by hiding from aggressors, using 'protected threats' and alarm-calling as a distraction: Whiten & Byrne 1988; Byrne & Whiten 1990), and they can achieve different goals in the same way (grooming can be used to gain access to meat, tolerance, mates, infants and the products of a skilled individual's labour). What this suggests in turn is that social life does not 'present any single cognitive challenge; challenges change with the nature of social interactions' (Strum *et al.* 1997, p. 69).

The word that best describes the behavioural response to such challenges is, we think, 'expedience', by which we mean the ability to select whatever tactic is necessary to solve an immediate problem, regardless of the possible long-term consequences of such action. Expedience characterizes the social decisions of both monkeys and apes and is a concept that encompasses all forms of social intelligence, whether cooperative or competitive (see also Miller 1997 who uses the term 'protean'). It is also a way of thinking about primate social engagement, at least among the monkeys, that does not make unrealistic cognitive demands of the participants (Cheney & Seyfarth 1990).

The notion of expedience also embraces the actions classed as 'tactical deception' (e.g. Whiten & Byrne 1988; Byrne & Whiten 1990; Byrne & Corp 2004). Defined as behaviour from the normal repertoire used in a context where it can serve to mislead another animal, tactical deception exemplifies opportunism in the face of an immediate and pressing problem. Opportunism in this reading reflects not only the obvious negative connotation, but also the positive sense of making use of an opportunity that presents itself. Similarly, 'behavioural innovation' (the ability to respond to novel circumstances or stresses with new behaviours, a feature which correlates with the size of the executive brain: Reader & Laland 2001, 2002), falls under the same rubric.

To our mind, 'expedient, quotidian cognition', while less catchy, describes primate capabilities more accurately than 'Machiavellian intelligence', is more precise than mere 'social intelligence' and leaves open the possibility that other, non-social, selective forces have also operated on primate brains (Reader & Laland 2002; Seyfarth & Cheney 2002). For example, most behavioural innovations concern foraging (Reader & Laland 2001) and there is evidence to suggest that feeding on particular food stuffs may exert selection pressures to acquire particular cognitive skills (Stevens *et al.* 2004). It may be that socially expedient behaviour has its deep roots in this kind of ecological expedience (Noë 2005) and, as Kaplan & Robson (2002) suggest, may have helped to set up a synergy between brain size and longevity that resulted in the extended lifespan and large neocortex found in modern humans.

5. EMBODIED, DISTRIBUTED COGNITION

Clark's Law: "Everything leaks" Andy Clark, Edge website (2004)

The idea of primates as expedient actors embedded in their social groups also raises questions about the 'location' of cognition. The traditional focus of the Machiavellian intelligence/social brain hypothesis on

relationship-tracking and strategic decision-making is essentially Cartesian. It takes as its starting point a (thinking) subject in a world of objects, so that the central questions are inevitably directed at how subjects gain knowledge of, and relate to, the world and how minds gain knowledge of other minds. The metaphorical use of Machiavelli adds to this impression, where Machiavelli's objective observations on the court, and his advice to the prince, represent the mind of the monkey advising on the next move that the animal should make. Drawing on work in cognitive science, artificial intelligence and robotics, particularly that of Brooks (1999; see also Clark 1997; Dourish 2001; Anderson 2005), our view is that we should shift emphasis and recognize the embodied and situated (or distributed) nature of primate social cognition. A digression to consider the paradoxical behaviour of the tuna fish (Clark 1997) may help explain things more clearly.

Physiological studies reveal that the blue fin tuna (*Thunnus thynnus*) should not be able to swim as fast as it actually does. Studies by fluid dynamicists, however, show that tuna are able to find naturally occurring currents in the water, and then use their tails to create additional vortices, which they exploit for extra propulsion (Triantafyllou & Triantafyllou 1995). As Clark (1997) neatly suggests, the 'real swimming machine' is not the tuna alone, but the tuna 'in its proper context'—the tuna, plus the water, plus the vortices it creates and exploits. As for tuna, so for primates: the real 'social intelligence machine' is the primate acting in its proper context—its social group.

This has two implications for how we view primate cognition. The first is the emphasis on active engagement with the world and the recognition that cognition must therefore be embodied: that is, how animals represent the world must be grounded in the physical skills and experiences of their bodies as they act in it (Heidigger 1927; Brooks 1999; Lakoff & Johnson 1999; Anderson 2005). The mechanisms that control perception and action are thus linked to, and constrain, higher cognitive capacities. As Merleau-Ponty (1962/2002) stated, representations of the world are '...controlled by the acting body itself, by an 'I can' and not an 'I think that'' (see also Anderson 2005). This, in turn, means that there is no principled distinction between perception and cognition, thought and action.

This approach gives us a more appropriate evolutionary focus since, as Brooks (1999) points out, evolution has concentrated most of its time on developing the systems that perceive and direct action in a dynamic environment so as to ensure survival and reproduction, while higher cognitive faculties like '...problem-solving behaviour, language, expert knowledge and application, and reason' all appear late in the day, and must therefore be 'pretty simple once the essence of being and reacting are available' (p. 116). To understand cognitive processes one must therefore understand how they are rooted in bodily experience and interwoven with bodily action and interaction with other individuals (Merleau-Ponty 1962/2002; Varela *et al.* 1991; Clark 1997; Lakoff & Johnson 1999; Damasio 2004; Garbarini & Adenzato 2004; Anderson 2005)—a point to which we return below.

The fact that bodily experiences include interactions with other individuals brings us to the second implication for our view of primate cognition, which is that cognition is 'situated' and 'distributed'. Cognition is not limited by

the 'skin and skull' of the individual (Clark 1997), but uses resources and materials in the environment in the same way that tuna use vortices. The dynamic social interactions of primates are thus 'not pointers to a private cognition' (Johnson 2001, p. 168) but can be investigated as cognitive processes in themselves. It is important to note that by distributed we are not merely referring to social learning processes and 'cultural' behaviours. A distributed approach goes further in that it considers all cognitive processes to emerge from the interactions between individuals, and between individuals and the world. This links back to our characterization of primate social cognition as 'quotidian' since it requires that we pay attention to how social actors deal with, and solve, in practical terms, the mundane, routine problems they encounter (see Dourish 2001 for examples of this with respect to human cognition).

Johnson (2001) provides an excellent overview of how approaches to distributed cognition can be applied to primate behaviour. Her essential point is that a distributed approach allows ethology to emerge as a 'cognitive' as well as a natural science, one that does not exclude identifying the nature of primate mental representation, but which does not make it the sole focus either. By studying in detail the manner in which animals coordinate their behaviour and participate in social life, we can learn about what is salient to them in the both the social and physical world, and how the feedback gained from other animals and the environment leads to different trajectories of behaviour, both producing different outcomes and allowing new behaviours to emerge (Johnson 2001; see also Rumbaugh & Washburn 2003 whose notion of 'rational behaviourism' is very similar). The approach has its roots in the ecological psychology of Gibson (1979) and draws heavily on his idea that the nature of the environment (including other animals) 'affords' particular opportunities for engagement, again emphasizing the inseparability of perception, action and cognition.

Understanding 'cognition in the wild' (Hutchins 1985)—how non-human animals co-construct their knowledge of each other and the environment—will reveal how their decisions reflect specific social and physical affordances (Johnson 2001). To do so, we will need to identify what animals attend to when they act in the world (e.g. gaze direction, body orientation, threat and submissive displays, the relative positions of other animals, and potential escape routes or lack of them). For example, Kummer's (1968) classic description of movement decisions in hamadryas baboons (*Papio hamadryas hamadryas*), although not directly intended as such, is a good illustration of the distributed approach.

The direction in which the baboon band leaves the sleeping cliff each day is determined through an embodied 'voting exercise' in which one or more males 'proposes' a departure vector (Kummer 1968). This begins when a male moves along the vector to the periphery and sits facing away from the group. This is closely watched by other males who may then 'notify' an initiator by approaching, performing a hindquarter presentation and then moving off quickly along their own favoured route. Other males, with their associated females and offspring, then begin to aggregate behind one or other of the initiators so that, over time, the majority come to be oriented in a particular direction, at which point the band

departs. Various attempts at achieving behavioural coordination are apparent in this process: as well as notifying, vocalizations, pacing, staring in a particular direction and moving ahead of the stationary band all attract the attention of other animals and induce them to follow the signalling animal.

It should be clear from this description that the decision to take a particular travel route cannot be attributed to any one individual, but is distributed across the band as a whole. This means that any attempt to understand the cognitive processes involved in travel decisions will be doomed if it focuses on individual cognition alone. The route is decided upon by a socially embedded, highly situated form of behavioural co-ordination, which means that to understand the cognitive processes involved it is more profitable to consider how animals attempt to attract the attention of others, when they do so, which tactics are most effective and why they are salient to others, since the decision about travel emerges as much from these social decisions as from any form of individual spatial cognition. While studies that do this are still few and far between, *Leca et al. (2003)* show very effectively how group movements in capuchin monkeys (*Cebus capucinus*) reflect exactly these kinds of social processes. Moreover, they show how different configurations and positions in the group (clumped versus dispersed, core versus periphery) afford different opportunities for influencing group movements. Similarly, the work of *Flack et al. (2005)* shows how the behaviour of certain key individuals creates affordances that enable other forms of behaviour to emerge by a process of social 'niche construction' (*Odling-Smee et al. 2003*).

The distributed nature of these kinds of decision-making processes may explain why laboratory experiments produce such different views of primate cognition to those derived from field studies. Whereas studies in the wild illustrate the broad scope and ingenuity of primate behaviour (*Byrne & Whiten 1988, 1990*), laboratory studies reveal its limits (*Heyes 1998*). By removing all the social and environmental scaffolding that supports much of cognition in the wild, laboratory experiments will inevitably fail to capture much of what we recognize as characteristically 'primate' about the cognition of monkeys and apes.

A more distributed approach to primate cognition, with its basis in bodily action and 'behaviour reading', also highlights the continuity of primate and human cognition. *Andrews (in preparation)*, for example, points out that much of our own ability to predict and explain the behaviour of others comes not from the application of a belief-desire psychology or mental simulation, as we tend to assume, but by using methods like trait attribution (e.g. a person who leaves a small tip is assumed to be mean and stingy) and inductive generalization (that is, we assume that people will generally do what they did on previous occasions). These are methods that, as *Andrews* notes, are equally available to non-human animals that lack knowledge of other minds, suggesting that we share our folk psychology with them to a greater extent than we may think (see also *Povinelli et al. 2000* who use a similar argument to argue that chimpanzee cognition is based on this kind of behaviour-reading and not belief-desire psychology). At the same time, however, a distributed approach recognizes that some aspects of human cognition, like language, provide new affordances that are not available to our non-linguistic cousins.

6. EMBODIED SIMULATION

The distributed approach also chimes better with findings from neurobiology. *Barton (1996, 1998; Barton & Dunbar 1997)*, in particular, has conducted a detailed series of studies to specify more precisely which parts of the neocortex have expanded over the course of primate evolution. These show that visual cortex (in particular, area V1) has undergone the greatest expansion, along with an enlargement of the parvocellular system (associated with the analysis of fine detail and colour). *Barton (1998)* therefore argues that the parvocellular system has been enhanced during primate evolution in order to process details of dynamic social stimuli, like facial expression, gaze direction and posture, and to give these emotional 'valence' via the connections with the amygdala (*Barton 1998; see also Perrett et al. 1990*). The idea that primate social intelligence resides in the recognition and response to visual signals provides strong justification for a distributed approach, especially given that, as *Barton* himself argues (*Barton & Dunbar 1997*), such findings confirm that we have no principled way of distinguishing between perceptual and cognitive evolution.

Work on 'mirror' and 'canonical' neurons also emphasizes the falsity of separating action, perception and cognition (e.g. *Di Pellegrino et al. 1992; Gallese et al. 1996, 2004; Rizzolatti et al. 1996; Fadiga et al. 1997*). As is now well known, mirror neurons fire both when an actor performs a specific motor action and also when this motor action is simply observed (*Gallese et al. 1996; Rizzolatti et al. 1996*), or heard (*Kohler et al. 2002*). Canonical neurons, in contrast, fire when an actor performs a motor action on an object and also when the object itself is merely observed. So, for example, when picking up a mug, 'whole hand grasping' neurons are activated, as they are again during passive observation of a mug. What this means is that the affordances of an object (its possibilities for action) are built directly into our perceptual representation of it (*Gibson 1979; Garbarini & Adenzato 2004*). Our concept of an object's function cannot be separated from our perception of it, because such concepts are an integral part of our perceptual motor representations.

Even more intriguingly, there is evidence from monkeys and humans that both goal-directed intentions towards an object (*Fogassi et al. 2005; Iacoboni et al. 2005*) and communicative facial actions (*Buccino et al. 2004; Ferrari et al. 2003*) are encoded into perceptual representations in the same way. Thus, our mental representations of the world, the objects and individuals within it, are fundamentally linked to the actions that bodies perform in the world. This, then, provides us with a sound neurobiological mechanism by which concepts are physically grounded in bodily action.

In a series of important papers, *Gallese (2001, 2003, 2005; Gallese et al. 2004)* has argued that this implicit, automatic and unconscious mechanism forms the basis for the understanding of others as goal-directed agents. By means of 'embodied simulation' one individual achieves 'intentional attunement' with another. Primate individuals are inherently linked to each other, because the actions that are performed by others are also 'owned' by the observer who generates, at the sub-personal neurobiological level, those same actions.

This fundamental ability of the motor system to 'resonate' when viewing the actions of others also extends

to emotions and sensations. For example, Hutchison *et al.* (1999) and Jackson *et al.* (2005) have shown, for humans, that perceiving pain in others activates the same areas of the brain, such as the anterior cingulate, anterior insula and the cerebellum, that are known to play a role in pain processing. Wickers *et al.* (2003), also for humans, have shown that perceiving facial expressions of disgust in others and experiencing disgust (through exposure to disgusting odorants) both activate the same area of the left anterior insula, while Keysers *et al.* (2004) have shown that the same neural networks are activated both by being touched and by observing the body of someone else being touched. This kind of unmediated, direct form of action and emotion understanding is seen by Gallese (2005) as a basic form of empathy, one which allows animals in possession of mirror mechanisms to establish a meaningful understanding of others and of themselves (see also Preston & de Waal 2002 for a similar argument in relation to primate cognition).

Significantly, this basic level of inter-subjectivity does not require any mental state understanding of others or overt conscious simulation of another's mental or emotional state. This, therefore, is likely to reflect the way in which monkeys view and respond to each other: as goal-directed agents whose intentions and emotions are socially meaningful but understood in an embodied, non-mentalistic fashion. This view also highlights another way in which cognition can be said to be distributed, since actions in the world resonate across individuals simultaneously and are not confined to the individual mind or body alone.

In this respect, the recent findings of Paukner *et al.* (2004) are both intriguing and suggestive. They found that pigtailed macaques (*Macaca nemestrina*) showed a visual preference for an experimenter that was imitating their object-directed actions, rather than for one that was performing temporally contingent but different actions. The authors suggest that the macaques implicitly recognized when they were being imitated, although there was no evidence that they explicitly understood the imitative intentions of the experimenter. This supports Gallese's notion of a basic, unconscious embodied resonance mechanism. It would be interesting to know whether imitative experimenters are preferred by the macaques as interaction partners in other contexts, since one could hypothesize that behavioural co-ordination serves to increase social bonding by inducing this kind of physical resonance. It is notable that certain social behaviours (e.g. coalition formation, when this occurs) often involve tightly co-ordinated, identical movements on the part of the actors (P. Henzi & L. Barrett, personal observation). It certainly seems to work for humans, even when faced with digital avatars (representations of people in virtual reality): Balienson & Yee (in press) have shown that human subjects find imitating avatars more persuasive and likeable than non-imitating ones, even though they could not explicitly detect the imitation (see also Chartrand & Bargh 1999). This work, plus Paukner *et al.*'s (2004) study, demonstrate that intentional attunement can be studied empirically, highlighting the link between Gallese's theory of embodied simulation and Johnson's (2001) distributed approach (see also Strum *et al.* 1997). Understanding how, when and why animals co-ordinate their behaviour may therefore reveal as much about underlying cognitive and neurobiological processes as

more conventional cognitive experiments (see also Noë in press for a similar argument concerning experimental work on cooperation). Finally, as Gallese (2005) suggests, this evolutionarily ancient mechanism is likely to have scaffolded the subsequent evolution of the kinds of complex, mentalizing mechanisms that humans are known to possess (Gallese & Goldman 1998).

It should now be clear that moving away from a view of primate cognition as one of abstract mental representation divorced from the body and the world, to a view in which primates are situated in their social groups, directly perceiving opportunities for action in the objects they observe, implicitly understanding the emotions and intentions of the other individuals they encounter, and using these affordances to 'enact' their worlds and bring about behaviour (Klin *et al.* 2003), provides us with a route out of the circularity that Gigerenzer (1997) identified.

It may also provide insight into the attributes that have allowed humans to be so evolutionarily successful. Perhaps our greatest opportunistic and prosocial innovation as group-living animals has been to distribute our cognition to an unprecedented level by storing essential information in other minds, instead merely of our own. Wegner *et al.* (1991), for example, have shown how couples in long-term relationships tend to take responsibility for particular kinds of knowledge (he programmes the video; she deals with the mortgage) in a manner that increases their efficiency as a unit. Wegner (1986) argues persuasively for the ubiquity of this kind of 'transactive memory' in all walks of human life, from intimate relations to large organizations (see also Surowiecki 2004). Wilson *et al.* (2004), taking an explicit evolutionary perspective, have similarly shown the value of 'thinking as a group'. Distributing our cognition into other minds and calling on this knowledge as part of highly cooperative endeavours seems to be the key to human culture (Richerson & Boyd 2005). Looking for its roots in the cooperative behaviour and distributed and embodied cognition of our primate cousins would now be a natural direction for the social intelligence hypothesis to take.

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