Social brains, simple minds: does social complexity really require cognitive complexity?

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The social brain hypothesis is a well-accepted and well-supported evolutionary theory of enlarged brain size in the non-human primates. Nevertheless, it tends to emphasize an anthropocentric view of social life and cognition. This often leads to confusion between ultimate and proximate mechanisms, and an over-reliance on a Cartesian, narratively structured view of the mind and social life, which in turn lead to views of social complexity that are congenial to our views of ourselves, rather than necessarily representative of primate social worlds. In this paper, we argue for greater attention to embodied and distributed theories of cognition, which get us away from current fixations on ‘theory of mind’ and other high-level anthropocentric constructions, and allow for the generation of testable hypotheses that combine neurobiology, psychology and behaviour in a mutually reinforcing manner.

Keywords: social complexity; primates; anthropocentrism; social brain; distributed cognition; embodied cognition

1. INTRODUCTION

The social intelligence (social brain) hypothesis states that the demands of social life selected for large brains within the primate order (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998). This rests, necessarily, on the assumption that social life is complex, where this complexity makes demands that can only be solved with the use of flexible, cognitive strategies in real-time, rather than evolved ‘rules-of-thumb’ (Byrne & Whiten 1988; Dunbar 1998). The evidence in favour of the social brain hypothesis is persuasive, but based largely on proxy measures for both intelligence and social complexity, such as brain size and group size (e.g. Dunbar 1992a, 1995, 1998; Joffe 1997; Byrne & Corp 2004).

While the social intelligence hypothesis is not solely directed at primates—it hypothesizes that all socially living species should show enlarged brain sizes relative to more solitary congeners—it nonetheless implies that primate social groups will, in some way, be more complex than those of other socially living animals: since primates have disproportionately large brains, the selection pressures coming from the social environment must therefore have been stronger.

There are a number of hypotheses and explanations as to what might increase the complexity of primate groups. All of these have hinged, in one way or another, on the view that primates are more ‘political’ than other animals—more Machiavellian—such that their interactions occur at a number of different levels, within individualized societies, and involve more complex, polyadic forms of social engagement (de Waal 1982, 1986; Byrne & Whiten 1988; Cords 1997; Dunbar 1998). Here, we argue that evidence in support of this assumption reflects our own unspoken, and often unrecognized, anthropocentric commitments. These commitments lead us to confuse proximate and ultimate explanations and to endorse a Cartesian and propositional view of the mind generally, and of social cognition in particular. We believe that there is merit in considering primates, not as hermetically sealed cogitators, but as agents whose social cognition is determined, at least in part, by their being both ‘embodied’ and socially ‘situated’ (Clark 1997; Anderson 2003).

2. SOCIAL LIFE AND SOCIAL COMPLEXITY

It is undoubtedly true that the diurnal anthropoid primates, monkeys in particular, are intensely social. They form permanent groups in which one sex or another generally spends its entire life, with the result that groups are composed of extended networks of both matrilinial and patrilinial kin (Dunbar 1988; Strier 1990). Group living is thought to represent an evolutionary response to predation risk (and infanticide; van Schaik & Kappeler 1997), while the internal structure of groups—the degree to which the sexes are related, the nature of dominance hierarchies, the patterning of grooming interactions between individuals, particularly females—is argued to be a response to ecological constraints, specifically to the level of competition for food within and between groups (van Schaik 1983; Dunbar 1988). Group size and structure therefore represent a balance between the centripetal force of predation risk and the centrifugal force of competition. This is assumed to have created a...
selection pressure on individuals to evolve strategies and tactics that alleviate the negative effects of competition on reproductive success. The social brain hypothesis dovetails neatly with this, since the proposed strategies involve the formation of ‘coalitions and alliances’ (Harcourt & de Waal 1992) that enable individual animals to combine forces and prevent other individuals from monopolizing resources.

Socio-ecological models are generally silent on whether such strategies represent some form of conscious cognitive processing (although see Dunbar 1984) or if they represent evolved strategies, where action derives from some rule-of-thumb that does not require overt, conscious calculation of goals and consequences. Nevertheless, the incorporation of the social brain hypothesis into socio-ecological explanations does weight them in favour of the former: the complexity of social life in primate groups must require some more complex form of cognitive assessment if the links between social life and behaviour are to underpin brain size.

This comes about, at least partly, because our reasoning runs from brains to behaviour, rather than the reverse: since we know that primates have big brains, it follows that they should be doing more with them than other animals. This being so, the social behaviours that we see are assumed to be built on high-level, flexible cognitive assessment, where driving selection has ratcheted up the capacity to meet strategy with counter-strategy, thereby establishing the relative complexity of primate groups. These more complex mechanisms are therefore assumed to require more brain tissue.

Coalition formation is commonly invoked to explain complexity of this kind because it decouples rank and power (de Waal 1982; Datta 1983). Although rank might derive initially from intrinsic resource holding potential, it can be augmented, and the decline of intrinsic ability compensated for, by the ‘extrinsic’ power acquired through coalitional relationships (Datta 1983; Chapais 1992). This makes life inherently more complex because strategizing individuals must then base their decisions not only on observables, such as the body size or the current whereabouts of others, but also on details of the differentiated relationships between individuals within the group.

Coalitions are thought to be cultivated and maintained through allogrooming (Dunbar 1998). Grooming represents an investment of time and effort by one individual in another that establishes a special relationship among associating animals and increases the probability of coalitional support at some indeterminate point in the future. Strong grooming bonds are signals of the likelihood of ‘unmitting mutual support’ (Dunbar 1988, 1998, see also Kummer 1968). As this is ‘the core process that gives primate social groups their internal structure and coherence’ (Dunbar 1998, p. 186), and because both grooming clique size and group size correlate with neocortex ratio (Dunbar 1998; Kudo & Dunbar 2001), it follows that cognitive complexity has been selected by the need to monitor and sustain one’s own grooming relationships, while simultaneously monitoring those of others across time in order to keep a running tally of their levels of extrinsic power (Dunbar 1988, 1998; Kudo & Dunbar 2001). This is a compelling proposition, supported by the apparently superior ability of higher primates to detect and identify third-party relationships (Dasser 1988; Cheney & Seyfarth 1990; Tomasello & Call 1997; Bergman et al. 2003).

### 3. Coalitions and Relationships

However, as we have argued elsewhere (Henzi & Barrett 1999; Barrett & Henzi 2002; Barrett & Henzi 2005, 2006), there is only equivocal evidence, at best, to support any causal link between grooming and coalition formation, while the formation of coalitions by adults against other adults is also rare in wild populations (Henzi & Barrett 1999; Silk et al. 2004). This is unexpected, given that such coalitions define the complexity of primate groups (Henzi & Barrett 1999). However, while the counterargument—that the rarity of coalitions belies their central importance (Silk et al. 2004)—works for other rare events, like predation or infanticide, it does not hold here. The risks of infanticide and predation form the selection pressures to which primates are thought to have evolved specific countermeasures, such as group-living itself (van Schaik 1983) and female promiscuity (Hrdy 1977). Female promiscuity and group-living are therefore common, which is why infanticide and predation are rare (Dunbar 1988). Coalitions, however, are not the selection pressure, but the evolved response to the selection pressure generated by resource competition. Coalitions should therefore be common and competitive rare, whereas the reverse is actually the case: there are many studies demonstrating the existence and extent of competition (see Strier 2002 for review), but very few establish a reliable, causal link between grooming and coalition formation in either the wild or captivity (see Cords 1997; Henzi & Barrett 1999). A recent study that explicitly set out to do so found no evidence of a direct link between the two (Silk et al. 2004), while grooming persists in the absence of coalitions (Barrett & Henzi 2006). This rarity of coalition formation, and the lack of a well-established link between coalitions and grooming, suggests that this behaviour is unlikely to represent a general explanation for the social complexity of primates and their groups.

It remains possible, of course, that monkeys sustain and monitor relationships for other valuable reasons besides coalition formation (see Silk et al. 2003a). Even so, the implicit assumption on which the argument rests—that monkeys can track their own and other relationships through time—has not been tested adequately (Cords 1997; Barrett & Henzi 2002). The point about tracking time is central to this argument because it is assumed that the obligate sociality imposed by predation risk entails, for each participant, a future in which competition is certain but its precise timing is unknown. Selection then favours a prospective cognition that can prepare for this uncertainty.

Of course, this ability is not necessary for relationships to be adaptive, as individuals could, in principle, achieve the same result with evolved rules-of-thumb that do not involve cognitive assessment. However, the
social brain hypothesis needs more than this, since non-cognitive, evolved rules-of-thumb do not require particularly large brains. The problem with assuming cognitive solutions that rely on some form of temporal projection is that monkeys, at least, despite large brains, seem to live very much in the here and now, and have yet to provide evidence that they can plan for future contingencies (Roberts 2002), inhibit inappropriate pre-potent responses (Chapais 1992) or remember when an event happened, in addition to what happened and where (Hampton et al. 2005).

There is also a lack of evidence to show that they can reason in a truly analogical, conceptual fashion (i.e. understand relations between relations), which would limit their ability to understand the equivalence between their own bonds and those of others (Thompson & Oden 2000). Dasser’s (1988) classic study, indicating that female macaques can understand bonds conceptually, does not rule out some form of perceptual matching between individuals, nor are the simple discrimination testing and match-to-sample designs sufficient to show relational matching (Thompson 1995; Thompson & Oden 2000). The two successful monkeys in Dasser’s (1988) study were not asked to match mother–offspring pairs with other mother–offspring pairs (i.e. to judge relations between relations by first identifying identity versus non-identity pairs and then matching appropriately on the basis of these relations), but only to match a picture of a mother with one of the two potential offspring, or to discriminate between a picture of a mother–offspring pair and a non-mother–offspring pair. The finding that chimpanzees can accurately match unfamiliar mothers with their offspring suggests that perceptual matching is a possible explanation for Dasser’s results (Vokey et al. 2004), while subsequent studies of monkeys using the appropriate relational tasks have not found evidence of analogical reasoning, although they used only physical matching tasks (geometric shapes) and not social ones (Thompson & Oden 2000). These findings contrast with observational and field experimental evidence, indicating that monkeys behave as though they do recognize third-party relationships (Tomasello & Call 1997), but whether this amounts to true conceptual, abstract understanding has not specifically been addressed. At least one study demonstrates that simple, associative rules-of-thumb can underpin this ability (Range & Noé 2005).

When Humphrey (1976, p. 309) originally proposed the evolution of a specifically social intelligence, he suggested that primates inhabit a world ‘where the evidence on which their calculations are based is ephemeral, ambiguous and liable to change, not least as a consequence of their own actions’. Here, as Carrithers (1991) notes, use of words like ‘ephemeral’ serve to emphasize the close temporal horizons over which monkeys must perceive and act on events, and does not argue specifically for foresight and intentional planning. There is little doubt that selection has produced cognitive abilities that allow individuals to perceive and respond appropriately to fast-acting dynamic changes in others’ behaviour (Barrett & Henzi 2005), but there is no a priori reason why selection should have acted to extend these abilities in time. The ability to respond flexibly and expediently to others’ behaviour does not demand the ability to plot and plan in any meta-representational fashion.

This all raises an obvious question: given the lack of clear empirical support, why do we persist with this particular view of primate complexity and the social brain? It seems to us that there is something unusually beguiling about the structure and form of the social brain hypothesis that has led us all to take a good deal of it on trust. One reason for this, of course, is that it possesses a very coherent internal logic that binds together two empirically undisputed endpoints (forced sociality; large brains) by means of some direct and intuitively appealing links between behavioural complexity and cognition. There is a clear, if implicit, equation of functional behavioural complexity with underlying mechanistic cognitive complexity, without demonstration (or even argument) of what kinds of mechanistic complexity are actually needed to produce behavioural complexity (or that they are needed at all). If so, it might be useful to ask why these links are so appealing.

Our answer to this question is that the reassuring congeniality of the social brain hypothesis is a direct consequence of the manner in which our own social cognition is built, i.e. we somehow see our former selves very clearly in this picture of primate social life. Indeed, it is our attempt to explain the evolution of human brains that drives, in part at least, the whole social brain project. Crucially, as is often pointed out (inter alia Wittgenstein 1968), although we ostensibly look on dispassionately, we can actually do so only through our own socio-cognitive spectacles. There is abundant evidence that we are heavily prone to perceiving and interpreting other components of the world, besides ourselves, in anthropocentric terms. As a result, we may impose complexity on a system that lacks it (or at least lacks the kind of complexity we usually attribute to it). In the case of the social brain hypothesis, we may inadvertently have used primates as a kind of tautological instrument: we have told them what we want them to be in order to validate our own view of who we think we are.

So what facets of human social cognition are important and into what assumptions are we consequently tempted? Answers to these questions may both reveal the commitments that certain arguments and hypotheses entail with respect to social complexity and illustrate how they might mislead us if they remain subliminal and unacknowledged. There are three particular facets of human cognition that we should consider: our inevitably anthropocentric attitude to the world; the way in which this leads us to view other species anthropomorphically; and the manner in which we structure our world as narrative. The first two lead us to view the worlds of other primates, and other species in general, in ways that resonate for us, while we artificially impose an extra layer of order on their worlds by means of the latter.

4. ANTHROPOCENTRISM AND ANTHROPOMORPHISM

An anthropocentric stance is something from which, to a large degree, we cannot retreat: by definition, neither can we see the world in anything other than human
This bias can work both ways. In addition to ascribing human attributes to other animals inappropriately, we can also deny them certain cognitive capacities in an equally inappropriate manner, because we confuse what is necessarily required with the specific form these capacities happen to take in humans. The objections raised with respect to episodic memory in non-human animals are a case in point (Suddendorf & Busby 2003). Here, aspects of episodic memory, such as autonoæsis, which can only ever be demonstrated empirically in humans, were made an integral and essential part of its definition. To criticize any claims for avian episodic memory (Clayton et al. 2003a) by arguing that episodic memory is partly defined by elements that ‘belong’ to humans necessarily prescribes the investigation. The real issue, of course, is whether episodic memory is a cognitive mechanism available to other species, not whether other animals have a specifically human episodic memory. It should be obvious that they do not, since they are not human and, as Clayton et al. (2003a, p. 437) point out, it is inappropriate to insist that episodic memory should be defined by ‘the phenomenology of the modern human mind, rather than in terms of core cognitive capacities’: to do so is just anthropocentric narrow-mindedness.

The argument that anthropocentrism obscures the social lives of primates is not, therefore, a simple criticism of an ‘anthropomorphic’ approach per se: there is no reason why, taking an evolutionarily grounded view of cognition, other species should not also manifest some of the same cognitive capacities as humans, either by descent or convergence. This being so, we need to avoid an approach to animal sociality that places humans at the comparative centre. We should, instead, ask questions about what it means to be a living being of any kind, rather than immediately restricting ourselves to some comparison with humans. The proposition is, then, that anthropocentrism, whether positively or negatively anthropomorphic, needs to be acknowledged and contained because it denies animals their own voices.

In the case of social cognition, anthropocentrism leads us to ask questions about other primates’ social cognition from an unduly distorted perspective. This is one that privileges conscious, ‘higher’ forms of cognition, based on language and meta-representational ‘theory of mind’ (ToM) skills, because we think of these as essential and fundamental to the understanding of the behaviour of other humans, even though this is not generally the case (Liberman et al. 2002; Hutto 2004; Andrews 2005; Gallagher 2005). We consequently gear our research efforts explicitly to detecting these abilities or, more commonly, their precursors, in monkeys and apes, either as a check on our own uniqueness and/or as a means of identifying how our own skills in these domains have been derived from evolutionarily simpler mechanisms (e.g. Dunbar 1996; Bergman et al. 2003; Povinelli & Vonk 2003; Tomasello et al. 2003; Zuberbühler 2003; Cheney & Seyfarth 2005).

A research strategy of this kind requires commitments that, on reflection, might be problematic. Looking explicitly for precursors of human socio-cognitive attributes, for one, judges primate capacities
against a human standard and therefore necessarily sees in them some fraction of this standard at best, where these might better be regarded as adaptations in their own right (Tyler 2003). Adopting a ‘folk-theoretic’ stance that places unobservable mental states to the fore, another, creates all kinds of problems about how to define such states and justify their inference on the basis of observable behaviour (Johnson & Oswald 2001, p. 454; Povinelli & Vonk 2003; Andrews 2005). Finally, an emphasis on higher cognition leads to a neglect of the perception–action mechanisms by which animals actually engage with the world, on which selection has acted for a much longer period, and from which these higher-level processes emerge (Brooks 1999). This is the most relevant problem from our point of view because, by placing social cognition firmly ‘in the head’ as an abstract, logical, disembodied process, we ignore differences in active, bodily engagement with the world. So, when de Waal (2005) argues that Georgia, the chimpanzee, should be regarded as possessing a ‘complex and familiar inner life’ because her behaviour looks so very similar to our own, it disregards the fact that her body interacts with the world very differently from the ways that ours do. How might our own physical grounding of concepts differ if we could use our feet as effectively as our hands (or if we had flippers or a wholly carnivorous diet)?

6. WHOSE COMPLEXITY IS IT?

With respect to primate sociality, our narrative tendencies are most clearly revealed by the fact that anybody who has worked on primates will have found themselves, at one time or another, describing the life of a primate group as a ‘soap opera’—an on-going open-ended narrative involving a familiar set of characters (e.g. Dunbar 1996, p. 28). The question, of course, is: do other animals see themselves in this way? It is our view that narrative structuring is not part of the world of at least one primate group—the monkeys—and that when we impose a narrative structure on their social interactions, we make their worlds more complex than is warranted.

Hinde (1976, 1983) identified three levels of social structure: interactions (between particular individuals), relationships (the frequency, quality and patterning of these interactions over time) and social structure (the overall patterning of relationships within the group). Although he saw relationships as emergent, irreducible phenomena, Hinde also emphasized their fluidity, regarding them as dynamic equilibria in which an impression of stability can be created by the contingent shifts and adjustments in interactions. As Silk (2002) suggests, however, we have largely assumed that such irreducible social relationships exist, rather than providing well-defined, rigorous means of identifying them (see also Cords 1997). Despite this, they have come increasingly to be seen as evermore stable entities that, as we know, can be subdivided into such forms as ‘friendships’ (Silk 2002), ‘coalitions’ (Dunbar 1984, 1988) or ‘alliances’ (Harcourt & de Waal 1992) that animals sustain consistently and cooperatively. Consequently, whereas grooming and proximity maintenance (two measures of affiliation) might once have been viewed as constituting the relationship in and of themselves, they are now more often regarded as an index of some underlying bond that exceeds the sum of its parts. This, in turn, may reflect the fact that, to identify relationships, we abstract many interactions over time, therefore adding a temporal component, and temporal consistency, to our analyses of monkey life (which actually reflects an arbitrary, human-relative time frame, rather than one relevant to the animals themselves). In this way, the grooming we record between animals now can token ‘unstinting mutual support’ in the future (Harcourt 1992; Dunbar 1998).

This, however, amounts to the reification of a relationship concept that we still need to show has more than human significance (Barrett & Henzi 2002; Silk 2002).

The well-documented demonstration that social animals can reconcile after aggression (de Waal & van Rooymalen 1979; de Waal 1989) has helped bed down
this supposition that individuals service and repair their relationships in order to sustain them (Aureli & de Waal 2000). The recent finding that the lifetime reproductive success of female baboons increases with their sociability links all these elements together evolutionarily, and further suggests that selection could act on the psychological mechanisms that support these differing forms of association (Silk et al. 2003a). This, as already mentioned, is argued to drive complexity: the cultivation of relationships, while simultaneously monitoring those of others, places a significant cognitive burden on participants who track their status through time, and who pick up social knowledge and information that is not vital at the time, but can be used adaptively later on (Harcourt 1988, 1989, 1992; Whiten 2000).

If this is so, how might this social knowledge be constructed? Cheney & Seyfarth (2005, p. 152), for example, have used a suite of rigorous playback experiments to argue that wild female baboons’ ‘...knowledge is propositional’. By this, apparently they mean that it is a declarative, explicit form of knowledge (i.e. ‘knowing that’ an individual A has a relationship with B), rather than an implicit, procedural knowledge of others (i.e. ‘knowing how’ to engage with others, without any explicit understanding of their relationships). The empirical data comprise the time an animal spends looking towards a hidden speaker. Longer looking times are said to indicate the ‘parsing of narratives’ is already built into the cognitive mechanism underlying this looking time and further suggests that selection could act on the psychological mechanisms that support these differing forms of association (Silk et al. 2003a). This, as already mentioned, is argued to drive complexity: the cultivation of relationships, while simultaneously monitoring those of others, places a significant cognitive burden on participants who track their status through time, and who pick up social knowledge and information that is not vital at the time, but can be used adaptively later on (Harcourt 1988, 1989, 1992; Whiten 2000).

Finally, recent analyses of baboon social networks show that these do not have the temporal durability that is usually assumed. When food is abundant, females from two markedly different environments forego ‘companionships’ (sense Whitehead 1995) and like herding antelope are perhaps better regarded as merely gregarious. Only when food is scarce do the ‘constant companionships’ indicative of strong, differentiated relationships emerge. For part of each year, then, adult female baboons down-grade the qualitative status of their associations from what we would see as relationships to what network analysis reveals as ‘casual acquaintances’ (Henzi et al., Submitted). There is no suggestion that the phases without companionships trigger either temporary or permanent fission. This being so, models of social life that are predicated on the value of grooming effort as a bonding agent may benefit from reconsideration (Dunbar 199926). If relationships can regularly dissolve without affecting group integrity, it is hard to see why imposed reductions in social time should inevitably lead to group fission as these models predict, and why group size should necessarily be limited by cognitive constraints on relationship tracking.

Overall, then, these findings suggest that the need for individuals to service, protect and repair relationships through time may have been overestimated, for wild populations at least. This is reinforced by the fact that most data in support of grooming bonds come from Old World monkeys; studies of New World primates have shown that grooming is much less common, despite group and brain sizes similar to those found in Old World species (Strier 2002). In captivity, from where much of the data on relationship value come (e.g. Cords 1997; de Waal 2003 for reviews), individuals may well need to ensure that they sustain contact with others owing to an absence of alternative responses to aggression. At the same time, of course, they have more time to engage in social interaction and little else to occupy them. This, in itself, is interesting and shows that primates have the flexibility to adopt a variety of social solutions to their quotidian problems. We argue, in fact, that this kind of behavioural flexibility is the key to
understanding primate social adaptation (Barrett & Henzi 2005). The construal of primate social engagement in terms of narrative relationships, on the other hand, seems comparatively less secure. At the very least, these concerns suggest that we should be sceptical about assuming that monkeys see their relationships as we see them.

7. THE INTERPRETATIVE GAP

If we cannot avoid our own socio-cognitive biases, and acknowledge that they might lead us astray, we are obliged to find a way to proceed. The most sensible approach is probably to acknowledge the gravitational pull of an anthropocentric narrative and to ask explicitly how something might be achieved if it is not being achieved in a human-like way. What we have to do, in other words, is to deal with Dennett’s ‘interpretative gap’.

As Dennett (1989) has made clear, we adopt a stance when we predict or explain a system. Whereas we might accurately predict the behaviour of a baboon by ascribing reason to its actions (the ‘intentional stance’), which natural selection licenses us to do, this does not naturally entitle us to use reason as an explanation of the action (see also Kennedy 1992). Or to put it more simply, it is not necessarily the case that an animal which behaves ‘as if’ it is thinking, actually is. Or if it is, there is no need for it to be doing so in the way that we do (Povinelli et al. 2000). Although the intentional stance is unavoidable (Dennett 1989), it necessarily opens up an interpretative gap—between prediction and explanation, and between function and mechanism—that must be closed. Our argument, then, is that the current conception of the social intelligence/social brain hypothesis inevitably opens up the interpretative gap because it is a hypothesis that elides evolutionary response with proximate mechanism, and allows evidence for the former to be taken as support for the latter.

The original social intelligence hypothesis, as put forward by Jolly (1966) and Humphrey (1976), was a strongly evolutionary hypothesis, which aimed to explain why primates were more brainy than other animals, despite the fact that the environmental challenges facing them were no more taxing, and sometimes considerably less so, than those that faced other species. The hypothesis put forward was that the social environment provided the cognitive challenges, so that improvement in cognitive ability in one part of the population would over time ratchet up the level in the rest of the population due to the interactive and dynamic nature of social engagement, with the smartest animals enjoying increased survival and reproductive success. As we have shown, the behaviours assumed to have been selected were those associated with relationship formation, maintenance and protection (which were also seen as characteristic of primates), and these in turn were assumed to require certain sophisticated cognitive capacities, based largely on a folk psychological projection of our own abilities in these domains (see also Silk 2002) for a similar argument with respect to the evolution of reconciliation.

Consequently, evidence in support of the evolutionary argument, such as the correlation between group size and brain size across the primate order (Dunbar 1995), has also been taken as implicit support for the postulated proximate behavioural and cognitive mechanisms by which individual animals increase survival and reproductive success. But such evidence does not, and cannot, tell us anything directly about proximate mechanisms. Moreover, the same is true even if we move down a level and show that the behaviours themselves are deployed by females in a way that is directly fitness enhancing (e.g. Silk et al. 2003a). This is because females that act as if they know their relationships are valuable and worth protecting may well be doing so in an evolutionary sense, but not necessarily at a more proximate level: the selection pressures acting on the actual cognitive mechanisms by which females engage with each other may be very different from the evolutionary forces that have shaped fitness-enhancing sociability in general. The successful application of our own folk psychological understanding of primates to generate functional hypotheses and explanations of behaviour cannot, therefore, be taken to indicate that we understand anything about the psychological mechanisms that primates might use to understand each other.

One way that researchers have used to get around the problem of the interpretative gap is by appealing to phylogenetic similarity and, in essence, closing the gap by fiat. Consequently, de Waal (2001, p. 70), for one of many examples, argues that the ‘mere five to six million years’ which separate chimpanzees and humans shift the burden of proof (concerning behavioural or cognitive similarities) to those who deny the relevance of this fact: ‘But doesn’t …parsimony argue against assuming a huge cognitive gap when the evolutionary distance between humans and apes is so small’ (de Waal 1997, p. 53). Interestingly, in this regard, baboons emerged as a species only some 2.5 Myr ago. Nevertheless, they have subsequently differentiated into a number of forms that are distinctively different in behaviour. Here, an assumption of interpretative continuity can—and has—lead to misinterpretation (Henzi & Barrett 2003). In truth, as Dennett has indicated, the interpretative gap is only narrowed by adopting the intentional stance and then setting out specifically to test its starting assumptions. The burden of proof, therefore, falls squarely on all of us, all of the time.

Therefore, if we begin by acknowledging explicitly our anthropocentric perspective, our objective must be an examination of the mechanisms by which we and other animals do the things that we do. In other words, our questions must become explicitly proximate mechanistic, and not evolutionary functional. We cannot use the ‘as if’ reasoning of functional hypotheses when asking questions about cognition because it blurs the distinction between proximate and ultimate explanation and makes it possible to slide between evolutionary and cognitive causes of action (Kennedy 1992). Arguing that baboons act ‘as if’ they are parsing calls into narratives or that Diana monkeys act ‘as if’ they recognize that chimpanzee alarm screams signalled the presence of a leopard’ (Zuberbuhler 2003, p. 283), actively avoids considering mechanism.
This is fine if our concerns are the assessment of functional (fitness-based) outcomes, but clearly problematic for an elaboration of cognitive evolution, which is the ostensible intention of many of these studies. Merely arguing that monkeys act ‘as if’ they understand the chimpanzee calls, for example, does not really get us anywhere because the ‘meaning’ of the vocalization, in this instance, is neither its function nor the proximate mechanism giving rise to it. It sits uneasily somewhere in between as an intentional heuristic that, sooner or later, has to get cashed out for a concrete explanation in terms of mechanism, as well as function.

It is important to stress that this pursuit of mechanism is not in any way a caricatured, radical behaviourist denial of higher-order cognition. Analytically, since it is the comparison of plausible competing hypotheses concerning the nature of underlying mechanisms, it would have, in fact, the welcome and opposite effect of ending the use of statistical null models as the benchmark against which ideas or propositions are assessed (see also Gigerenzer 2004). At present, highly cognitive hypotheses are tested against null models, which is the equivalent of saying: ‘we are testing whether *something* is happening in these animals’ heads, rather than *nothing*. Rejecting the null hypothesis, then, does not mean that the postulated cognitive mechanism has been shown to exist, only that a cognitive mechanism of some kind is operating, rather than a simple stimulus–response link. Identifying and pitting alternative cognitive mechanisms against each other is the only way to establish what kind of cognitive mechanism is actually being used, as studies of memory development in children (Russell & Thompson 2003) and prospective cognition in jays (Clayton & Dickinson 1999) illustrate to great effect.

Given this, the question then arises as to where these alternative kinds of plausible mechanisms might come from. Our approach in what follows is to suggest that apparent cognitive complexity may emerge from the interaction of brain, body and world, and is not merely due to the level of internal complexity the animal itself possesses.

### 8. COMPLEX SOCIAL SPACE

With respect to monkeys, and their social interactions, this means recognizing, first of all, that the shifting and varied encounters which we view anthropocentrically as the evolutionary precursors to human relationships, and which we have assumed to possess a significant temporal component, may, from the monkey’s perspective, be better conceptualized as a form of spatial pattern recognition. In other words, monkeys may engage each other in a highly action-centred, continuous, spatial jockeying for position and influence within the confines of the group, using social contact and proximity as a means to achieving immediate goals, and monitoring the concurrent actions of others, but without any conceptual, representational knowledge of what they are doing, or any projection of this through time.

If this is the case, then fission may not be the result of weakening and fragmentation of relationships, followed by fracturing along lines of least resistance (Dunbar 1992b), but may simply reflect the inability to maintain ongoing contact with all other group members as groups become larger and more spatially dispersed. Where animals are frequently separated by the need to find food, fission can emerge as a gradual mechanical process in which subgroups become increasingly spatially disjunct. The formation of new groups is likely to be hastened where sleeping sites are readily available and where perceived predation risk does not set a high lower limit on the size of foraging group an individual feels comfortable in.

Similarly, we can view coalitions as only one component of a suite of tactics that monkeys use when they offer immediate benefits for both parties, i.e. as short-term mutualism (e.g. Silk et al. 2004) and not as prospective investment governed by reciprocal altruism (e.g. Seyfarth & Cheney 1984). Reconfigured in this way, they can be seen as the presentation of a spatially integrated ‘united front’ by two or more animals, where current need drives conjoint action and reduces the social stress experienced by the participants. Maintenance of spatial proximity may, by the same token, function as a more ‘passive’ form of coalitionary support reducing the likelihood of displacement or aggression and reflecting an immediate, dynamic response to changes in spatial positioning. The tendency of many female-bonded species to groom up the dominance hierarchy may involve a similar tendency to seek tolerance around higher-ranked animals both for the benefits this may offer directly and to reduce the likelihood of interference by third parties while in a dominant’s zone of tolerance (e.g. Silk 1982).

Under these conditions, individuals do not need to hold abstract conceptual notions of ‘bonds’ or track others’ relationships because they can gauge circumstances directly by looking at what is happening around them: the spatial structuring of the animals in their environment may obviate the need for certain kinds of high-level processing in the animals themselves, and they can ‘use the world as its own best model’ as Brooks (1999) suggests (see also Gibson 1979). This kind of ‘just in time’ learning is both less costly and time consuming than the ‘just in case’ learning proposed by Whiten (2000), which requires much more complex internal models of the world for efficient functioning. It fits, too, with Silk’s (1996) proposal that reconciliation acts fundamentally as a short-term signal of benign intent. In all cases, such manoeuvring is performed in the ‘here and now’ and we do not need to infer any form of planning or anticipation of the future.

Rejection of a narrative component to primate relationships is not a rejection of the possibility of complex social engagement *per se*, but an expectation that any complexity will be dynamic and result from on-going spatial engagement in real-time. It need not be a consequence of the integration of information across many social events and many actors. New World primates, incidentally, are among the beneficiaries of this conception since the absence of a strong relationship between group size and grooming time in the platyrhines (Dunbar 1991) has led to suggestions that they may lack the strategic capabilities of the catarrhines. Thinking in terms of space, from a highly action-centred perspective, rather than about time and
representations, may give us new insights into the social engagement of all primates, while also shedding light on the differences between monkey and ape cognition (Barrett et al. 2003).

9. BEING IN THE WORLD
The second means of dealing with the interpretative gap is to reject the Cartesian viewpoint that places an intentional (anthropomorphic) stance to the fore. If we assume that relationships are temporally constructed narratives in the heads of the animals, and use the intentional stance to make predictions about behaviour, we are immediately drawn into a view of animals as ‘thinking subjects’ and so privilege questions that deal with how subjects gain knowledge of the world, how they relate to it and how they acquire an understanding of the social worlds of others. If instead we adopt a more embodied approach to cognition generally (Anderson 2003) and to primate social cognition in particular (Gallese 2001, 2005, 2006, 2007; Barrett & Henzi 2005), we move from thinking of ourselves and other animals as detached observers of the world, but as beings situated in the world, and inseparable from it (Heidegger 1927/1978). This immediately gives us greater purchase on the mechanisms by which animals actively cope with the world, because many of these will be visible to us in the form of perception–action loops, and not as invisible mental constructs.

This fits with findings from various areas of cognitive science, including computer science, artificial intelligence and robotics, which argue that we should think of brains and cognition as behaviour control systems, designed to help humans and other animals engage actively with the world, rather than reflect on it (Clark 1997; Brooks 1999). Representations of the world, therefore, will be grounded in an animal’s physical skills and bodily experiences (Anderson 2003). Such a perspective has a much stronger evolutionary flavour (Damasio 1994) and, by focusing on the physical means by which an animal engages with the world, it immediately reduces our anthropocentric tendencies. It allows us to discount the association of cognition with high-level thought processes alone and to study perception, action and cognition as a functionally integrated system (Barrett & Henzi 2005; Barton 2006, 2007). In so doing, it returns us to Leslie Brothers’ (1990) original concept of the social brain, where neural activity and bodily responses to social stimuli form the basic building blocks for participation in social acts, and therefore gets us away from the ‘neuroist’ approach that places all the important stuff solely in the brain itself (Brothers 2001).

As a consequence, embodied cognition (EC) places a different emphasis on evolutionary continuity. It proposes that we investigate the way in which perception-action mechanisms, and bodily engagement with the world, can exploit the structure of the environment (Gibson 1979) and so limit the need for expensive (often slow), high-level internal processing, as a cost-effective evolutionary process should (Humphrey 1976). More importantly, it turns an anthropocentric research strategy on its head by proposing that, instead of looking for the cognitive precursors of sophisticated human cognition, we should investigate the ways in which perception-action mechanisms constrain (in the sense of canalize) the evolution of high-level processes (Brooks 1999; Anderson 2003; see also Panksepp 1998).

An embodied perspective, therefore, moves us away from an anthropocentric, mentalistic view of cognition and extends it beyond ‘skin and skull’ to the body and the world (Clark 1997), with the aim of understanding how cognitive processes are rooted in bodily experience and interwoven with bodily action and interaction with other individuals (Merleau-Ponty 1962/2002; Varela et al. 1991; Damasio 1994; Clark 1997; Lakoff & Johnson 1999; Anderson 2003; Garbarini & Adenzato 2004; Barrett & Henzi 2005). It is therefore an approach that has much in common with the research strategy that Shettleworth (1998) characterizes as ecological; here the assumption is that evolution has selected for the behaviours and mechanisms that enable animals to cope with life in particular ecological niches. It acknowledges that animals may show skilled and sophisticated performance in specific domains, where they may be superior to humans, but that this need not manifest itself in other domains, indicate some general form of anthropocentrically defined ‘intelligence’ or reflect phylogenetic proximity to humans (as implicitly assumed by anthropocentric imperatives such as Morgan’s canon). The striking social and cognitive skills of corvids, for example (Clayton et al. 2003b; Emery & Clayton 2004), expressed in the context of food caching, can therefore be seen in this light. Similarly, the inability of Old World monkeys to match the cooperative behaviour and tool-use capacities of capuchin monkeys (e.g. Mendres & de Waal 2000; Moura et al. 2004) are a puzzle only if we adopt an anthropocentric, phylogenetic perspective.

There is strong neurobiological support for an embodied primate cognition (Perrett et al. 1990; Barton 1996, 1998; Rizzolatti et al. 1996; Gallese 2005, 2006, 2007; Gallese et al. 2004). This provides the necessary springboard from which to test the ‘physical grounding hypothesis’ (Brooks 1999), which is the central project of EC (Anderson 2003). Gallese (2001, 2003, 2005, 2006, 2007; Gallese et al. 2004), in particular, has presented an extremely compelling argument for mirror mechanisms (systems of motor and pre-motor neurons, activated by one’s own performance of action and the observations of others’ actions) as the basis of an implicit, automatic and unconscious understanding of others as goal-directed agents.

The fundamental ability of the motor system to resonate when viewing action (and that extends to emotions and sensations; see Gallese 2006, 2007, for a review) suggests that primates can establish a meaningful understanding of others, and of themselves, without any need for mental state understanding or overt conscious simulation. This is therefore a basic form of inter-subjectivity or empathy (Preston & de Waal 2002; Gallese 2005). As a result, individuals automatically generate affordances—possibilities for action—for the animals that observe them and
affordances that are built directly into an animal’s perceptual representations. Social engagement may not therefore require the ‘propositional’ knowledge that is often assumed (Zubereuhler 2003; Cheney & Seyfarth 2005). Social understanding may, instead, be a form of pattern recognition involving ‘active’ perception (Noë 2004). It will then be better modelled and understood as embodied in the patterns of activation of neuronal units, linked in distributed networks, than as some form of logical, syntactically organized computation (Clark 1993).

Mechanistic explanations of this type can explain why kin recognition in primates appears to be based on familiarity and not on more specialized mechanisms like phenotype matching (Rendall 2004). Since neural networks require experience, they have the flexibility to cope with changes in cue features over time (as naturally happens as individuals develop and age) lacked by the other more deterministic processes. Indeed, neural networks are the ‘cellular instantiation’ of familiarity: what the network ‘knows’ is that with which it is most familiar. The experiential plasticity of neural networks also allows a continuous updating of social signals, which can account for the proficiency with which animals can perceptually track changing social cues (Rendall 2004). This makes such mechanisms potentially more powerful than highly specialized mechanisms, because they are robust to deviations in cues or context. By contrast, the narrowly tuned, specialized mechanisms used by, e.g. ants and digger wasps, work extremely well in the correct context, but can be perturbed by the smallest deviation from normal triggering conditions, revealing themselves as robotic and ‘stupid’. Generalized mechanisms, as they are more flexible, allow for more flexible, contingent behaviour.

For long-lived social primates, for whom both physical and social environments are inherently unstable, such mechanisms are arguably more adaptive than specialized cognitive routines, such that we should expect flexible, experientially informed pattern-recognition to form the basis for much of primate cognition. The potential downside of such mechanisms is that they are tissue intensive: large-scale pattern recognizers require a lot of connectivity to implement (Clark 1993). In this case, however, it adds strength to our argument, since it is precisely this extra requirement for neural tissue that the social brain hypothesis must explain. While evolution is cost-effective, as Humphrey (1976) originally argued, this does not mean that it must also be an efficient engineer, as we tend to assume. Convoluted, messy solutions may be both plausible and can be tested. Monitoring the attention structure of such triads may tell us more about how individuals manage social engagement than does interpreting social responses in terms of abstract rank structure alone (e.g. Johnson & Oswald 2001). The study by Paukner et al. (2004) showing how pigtailed macaques preferred to watch a mimicking experimenter, despite no overt recognition of the mimicry, is therefore very interesting in this regard, since it flags up, quite literally, the salience of close social signals, which can account for the proficiency with which animals can perceptually track changing social cues (Rendall 2004). This makes such mechanisms potentially more powerful than highly specialized mechanisms, because they are robust to deviations in cues or context. By contrast, the narrowly tuned, specialized mechanisms used by, e.g. ants and digger wasps, work extremely well in the correct context, but can be perturbed by the smallest deviation from normal triggering conditions, revealing themselves as robotic and ‘stupid’. Generalized mechanisms, as they are more flexible, allow for more flexible, contingent behaviour.

Our take-home message, therefore, is that primate groups are not more socially complex than those of other animals per se, and it is not social complexity alone that has selected for greater brain size. Rather, these long-lived, group-living animals face significant changes in both social and ecological environments over the course of their lifespan, and synergistic effects between the two (Sterelny 2007). Consequently, they require high levels of behavioural flexibility (‘quotidian cognition’; Barrett & Henzi 2005), instantiated in generalized pattern-recognition networks, in order to survive.

The generation of hypotheses and predictions linked to pattern recognition argues for an increased focus on naturalistic, observational studies of primate social interaction—the manner in which individuals respond to the social cues of others, the cues they themselves display and how this leads to forms of behavioural coordination—rather than observations and experiments designed to tap into abstract, conceptual knowledge. The classic demonstration that monkeys understand rank relations, for example, does so by showing how the lower ranking of two individuals retreats at the approach of a third, higher-ranking female (Cheney & Seyfarth 1990). This is usually interpreted as an indication that individuals compute the rank relationships of others and do not rely on a purely egocentric assessment. It could equally, however, be achieved by a simpler embodied mechanism, more related to ‘intentional attunement’ (Gallese 2006, 2007) than to ‘propositional knowledge’ (Cheney & Seyfarth 2005). Individuals may attend to the salient features of the responses of others to particular events, generating distributed networks that can match these patterns when they recur. If the approaching female provides physical cues and directs her gaze more towards one female, the approached animals can respond in different ways, depending on whether they are the focus of attention and for how long this lasts. The lower-ranking female may show greater muscle tension, stiffen her posture, show facial expressions or make preparatory movements all of which enable the other female to infer an intention to leave and respond accordingly by remaining.

While this is crude conjecture, it is, in principle, plausible and can be tested. Monitoring the attention structure of such triads may tell us more about how individuals manage social engagement than does interpreting social responses in terms of abstract rank structure alone (e.g. Johnson & Oswald 2001). The study by Paukner et al. (2004) showing how pigtailed macaques preferred to watch a mimicking experimenter, despite no overt recognition of the mimicry, is therefore very interesting in this regard, since it flags up, quite literally, the salience of close behavioural coordination among partners. The findings of Chartrand & Bargh (1999) that similar non-conscious mimicry can facilitate intimacy in humans, perhaps forming the true ‘social glue’ which bonds groups (Lakin et al. 2003), therefore generate a testable prediction with regard to the behavioural coordination shown by monkey affiliates. Placing a stronger, more ethological focus on how individuals coordinate their behaviour under various conditions, we can begin to hypothesize and test how the mechanisms that govern how they perceive, act and move in such an environment are linked to the internal representations they generate: as Anderson (2003) states, representations are more likely to be governed by these practical criteria than by abstract or logical ones. Gallese (2007) is already making great strides in specifying how...
embodiment scaffolds representational schema and influences higher-order cognition (see also Gallesse & Goldman 1998; Gallesse et al. 2004). If behavioural studies also begin to pay more attention to the details of how animals perceive and act in the world, rather than what we think they think about it, then we can begin to consider seriously how ‘lower’ faculties might relate to ‘higher’ ones. Alternatively, as we argued above, they may reveal how the interleaving of perception and action in response to environmental structures eliminates the need for certain high-level forms of processing altogether (Brooks 1999), or at least greatly reduces the complexity of internal mechanisms.

Again, it is important to stress that this emphasis on embodied behaviour is not a return to *behaviourism*. This is because perception and action form ‘loopy structures’, where action generates perceptual feedback that, in turn, generates further action, so that outward behaviour becomes an important co-contributor to the processes, including neural processes, which generate further behavioural response (Keijzer 2005). As Hurley (1998) notes, by contrast, behaviourism assumes a linear, one-way process where perception causes action (i.e. input to output), but there is no further feedback from action to perception (i.e. output to input).

An embodied perspective, then, is one that allows us to consider social cognition as an observable, distributed event (Hutchins 1985; Brothers 2001; Johnson 2001), rather than as purely invisible, private ones. This view owes much to Heidigger (1927/1978), and the rejection of a ‘Cartesian homunculus peering out at the world and seeing what’s there’ (Dourish 2001, p. 108) in favour of a world that is already structured meaningfully through a process of common, social practice. By the same token, when monkeys are born into their groups, they encounter a world of common social practice and what they learn, over the course of development, is how to participate. This is something that is learned through participation itself (Dourish 2001; Anderson 2003).

For psychologists, this view goes back at least to Vygotsky (1978) and the idea that cognition initially begins by being social and visible and is only later internalized and invisible. Models of mental representation are not rejected by such a view, as some might suspect, but rather can ‘inform models of mental representation by charting ontogeny through embodied interactions in the infant and its caretaker, the juvenile and its cohorts and the adult and its society’ (Johnson 2002, p. 628). A distributed view, therefore, emphasizes that behaviour—or more accurately interaction—is the source and cause of what must ultimately end up inside the head (Johnson 2002). Moreover, despite reservations that a socially distributed view is only of any real relevance to humans (Tomasello & Call 1997, Strum et al. 1997), Johnson (2001) and Johnson & Oswald (2001) illustrate how this can be applied to other primate species.

In addition to other individuals, the surrounding physical environment provides cognitive resources. Objects in the environment present animals with certain ‘possibilities for action’ (Gibson 1979) and afford certain responses (e.g. for humans, a chair affords the possibility of sitting down on it). These affordances and their relation to ongoing activity can help us to understand how and why certain behaviours are played out in certain ways at certain times. Strum et al. (1997), for example, show how consort takeovers among male baboons are structured by the properties of the sleeping cliffs where these take place: the limits they place on movement can be used to a male’s advantage and lead to an unfolding of events quite different to those on the plains (see also Johnson & Oswald 2001 on ‘social tool use’ in bonobos). In this way, Machiavellian intelligence need not be Machiavellian in the sense that currently holds sway, because the flexibility, unpredictability and ingenuity shown by animals is due to processes that are distributed across brain, body and world.

The basic tenet of a distributed approach, therefore, is that dynamic social interactions do not merely point to internal cognitive acts but are cognitive acts in themselves (Kirsh 1996; Johnson 2001). Kirsh (1996) in particular distinguishes between ‘pragmatic acts’ that move an individual closer to a better state in the external environment, and ‘epistemic acts’ that move an individual to a better state in its cognitive environment. Epistemic acts, therefore, change the world in order to have useful cognitive effects on the actor; they create cognitive affordances that help improve the speed, accuracy or robustness of cognitive processes, rather than enable the agent to make literal progress in a task (Kirsh 1996). In humans, for example, moving Scrabble tiles around makes it easier to see the potential words that can be formed, and can therefore be considered an epistemic act. This close interleaving of physical and mental actions to reduce the complexity of a task means that it becomes important to pay attention to the means by which an individual tackles a particular task, because the task is carried out partly in the individual’s head and partly in its environment. The degree to which primates and other species engage in any kind of epistemic action is an empirical issue at present, largely because we have not looked for these kinds of behaviours in order to understand cognitive processes.

It should be readily apparent how this kind of behaviourally oriented approach can also be used to test and develop the theories of intentional attunement and embodied simulation that emanate from neurobiology (Gallesse 2006, 2007). Mirror systems, in particular, show us how, at the most fundamental neuronal level, our understanding of others is a distributed process that requires action in the world. Hopefully, a better understanding of the embodied and distributed nature of social cognition in our fellow primates will enable us to understand them on their own terms. Tying this to work demonstrating the embodied and distributed nature of cognition in humans (e.g. Varela et al. 1991; Vygotsky 1978; Fogel 1993; Gallagher 2005) may then enable us to identify true commonalities across species, rather than anthropocentric chimera.

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