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Primate Social Cognition

Uniquely primate, uniquely social, or just unique?

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Abstract: Primates undoubtedly have impressive abilities in perceiving, recognising, understanding and interpreting other individuals, their ranks and relationships; they learn rapidly in social situations, employ both deceptive and cooperative tactics to manipulate companions, and distinguish others' knowledge from ignorance. Some evidence suggests that great apes recognize the cognitive basis of manipulative tactics and have a deeper appreciation of intention and cooperation than monkeys; and only great apes among primates show any understanding of the concept of self. None of these abilities is unique to primates, however. We distinguish (1) a package of quantitative advantages in social sophistication, evident in several broad mammalian taxa, in which neocortical enlargement is associated with social group size; from (2) a qualitative difference in understanding found in several distantly related but large-brained species, including great apes, some corvids, and perhaps elephants, dolphins, and domestic dogs. Convergence of similar abilities in widely divergent taxa should enable their cognitive basis and evolutionary origins to be determined. Cortical enlargement seems to have been evolutionarily selected by social challenges, although it confers intellectual benefits in other domains also; most likely the mechanism is more efficient memory. The taxonomic distribution of qualitatively special social skills does not point to an evolutionary origin in social challenges, and may be more closely linked to a need to acquire novel ways of dealing with the physical world; but at present research on this question remains in its infancy. In the case of great apes, their ability to learn new manual routines by parsing action components may also account for their qualitatively different social skills, suggesting that any strict partition of physical and social cognition is likely to be misleading.

Introduction

Fifty years ago, human experimental psychology was dominated by learning theory: but the ‘cognitive revolution’ dramatically changed the nature of research into human behaviour. Since then, neuroscientists have regularly used non-human primates as a ‘simpler’ model to test theories of human social cognition and information processing, with most laboratory studies of primates relying on a few species of macaque monkeys. During the same period, a growing number of psychologists, anthropologists and ethologists began studying the social behaviour of a wide range of non-human primates, both in the primates’ natural habitat and in the laboratory, in a parallel attempt to reconstruct the evolutionary history of human mental competence.

In this review, we shall attempt to explain what these wider-ranging studies have shown us about non-human primate social cognition, in the hope that it will inform understanding in neuroscience and new work on humans. It is important to note there are numerous differences in behaviour between different primate species, even among different species of monkeys—as well as between monkeys and great apes, of which humans are one of several extant species including orangutans, gorillas and chimpanzees. These differences may reflect variations in the cognitive architecture, or they may result from socioecological differences between species that limit the expression of similar underlying cognitive capacity. Where appropriate, we therefore identify the primate species studied, in order to avoid the trap of treating all monkey species, or even all non-human primates, as alike in their behaviour and cognition.

Mimicking the paradigm shift in human experimental psychology, there has been a later and more gradual change towards cognitive explanations of animal behaviour.

Earlier debates about behaviour were often dominated by the issue of whether ‘simple’

associative learning could account for the data, or whether the animals ‘were cognitive’, usually taken to mean having conscious thought processes (Byrne and Bates, 2006; Macphail, 1998). As in the case of human experimental psychology, the associative approach was not refuted in principle, but the sheer effort and increasingly ad hoc appearance of associationist explanations for complex behaviour led to the ascendance of cognitive theorizing. A particular impetus for change came from the growing evidence of sophistication and complexity in primate behaviour: in taking account of a rich network of relationships (Cheney and Seyfarth, 1982a, 1986, 1990), in interpreting others’ intentions (Menzel, 1971, 1974; Premack, 1988; Premack and Woodruff, 1978), and in deploying subtle manipulative tactics (Byrne and Whiten, 1985, 1991, 1992; de Waal, 1982, 1986; Whiten and Byrne, 1988). By the mid 1990s it had become acceptable to compare across species by taking a generally cognitive approach, framed in terms of information processing rather than consciousness (Byrne, 1995; Tomasello and Call, 1997). This shift towards cognitive explanations of behaviour has now left us much better placed to generate and test hypotheses about the evolution of human cognitive skill.

Much of the new evidence of complexity in primate behaviour came from the social realm, and comparable sophistication was not known for physical cognition (Byrne and Whiten, 1988; Cheney and Seyfarth, 1985; Jolly, 1966). This pattern meshed with Humphrey’s influential theory (Humphrey, 1976, 1981) that the evolutionary challenge for which the solution is ‘intelligence’ is more likely a social than a physical one. He argued that semi-permanent social living, as found in many primate species, sets up a selective pressure for increasing social sophistication. The fact that the competitors are conspecifics causes a ‘ratchet effect’ in which intelligence increases continually. Support

for this line of theorizing has come from finding that the size of the primate brain—specifically, the neocortex—was closely related to measures of social group size (Dunbar, 1992a, 1993, 1995, 1998) and social skill (Byrne and Corp, 2004; Reader and Laland, 2001; Reader and Lefebvre, 2001).

In contrast to primates, most non-primate vertebrate taxa are found in groups where the membership is inconstant and there is no evidence that individuals recognize each other as distinct and base their interactions on this individuality: they are ‘herd animals’, but not truly social. (‘Hefted’ ungulates such as sheep, faithful to a small range during their whole lives, may however be more socially sophisticated than is often recognized: for instance, recognizing other individuals by their faces and voices: Kendrick et al., 1995), but so far little work on cognitive skills has been conducted on these animals.) Where groups are inconstant aggregations, relationships between brain size and typical group size are lacking (Emery et al., 2007; Shultz and Dunbar, 2006, 2007), adding further support to the idea of a close relationship between brain enlargement and semi-permanent social living—where groups are consistent in the long-term but membership can change over time, usually following rules such as one sex leaves the natal group at sexual maturity.

These lines of evidence led to a consensus view that the early evolution of human intelligence within the primate lineage derives from increasing social complexity, as indicated by concomitant increases in brain size—a hypothesis variously called ‘social intelligence’ (Humphrey, 1976), ‘Machiavellian intelligence’ (Byrne, 1996a; Byrne and Whiten, 1988) or the ‘social brain’ (Brothers, 1990; Dunbar, 1998). The corpus of data has grown rapidly in the last 15 years, enabling us to examine the strength of this consensus. Where appropriate, we examine these data against a background of evidence

from the increasing range of species that have now been studied in cognitive terms (e.g. corvid birds, such as scrub jays, ravens and magpies; carnivores such as domestic dogs, hyaenas and meerkats; and ungulates such as pigs, elephants and their cetacean relatives bottlenose dolphins).

Throughout the review, we use the everyday term ‘understand’ for the idea that the animal may represent meaning or unobservable causal connections in what it does or perceives; we treat understanding something as a matter of *taking account of its underlying meaning or causal role in an appropriate way*. There is of course a (human) sense of understanding which refers to private experience, and which we will therefore probably never know about in other animals. Moreover, because humans have the option of using language to recode and re-represent their experience, it is highly likely that no non-human ‘understands’ things in quite the way an adult human would. These inevitable differences mean that it remains possible to construct plausible alternative explanations for virtually all the data of this review, in terms that have no close relation to human cognition but derive from behaviourist philosophy and animal learning theory (Heyes, 1994, 1996, 1998; Macphail, 1985, 1998; Penn et al., 2008; Penn and Povinelli, 2007; Povinelli and Vonk, 2003). Our view is that, although explanations based on learning theory often provide valuable critical correction, and connectionist models of cognitive processes (in some ways the modern equivalent of the networks of unlabelled associations in behaviourist learning theory) have achieved notable successes in specific areas (e.g. Doi et al., 2009; Mayor and Plunkett, 2010), cognitive and neurocomputational explanations are not mutually exclusive, but instead provide different levels of explanation, each with different utility (Byrne and Bates, 2006). In any case, we consider it unlikely that disputes about the right approach to understanding the nature of cognition will be settled by logic

and decisive argument (Garzon and Rodriguez, 2009): which approach will prove more productive over time is an empirical question.

Primate abilities in the social realm

Knowledge of other individuals

We have learnt much of what an animal understands about its companions from field playback of vocalizations. Playback studies have enabled researchers to simulate signals from specific individuals, or interactions between specific partners, using the target animal's reaction as an index of what it knows. For example, playback studies have been used to study individual recognition in various animal species. Ground squirrels (*Spermophilus richardsonii*), marmots (*Marmota flaviventris*), and meerkats (*Suricata suricatta*) have all been shown to distinguish the identity of others from vocalisations. For marmots and ground squirrels, this allows individuals to determine whether alarm calls were given by reliable or unreliable group members (Blumstein et al., 2001; Hare and Atkins, 2001), but the function of this discrimination ability is not clear for meerkats (Schibler and Manser, 2007). Playback experiments have shown that monkeys are aware of the individual identity of others, and not only those individuals within their own group. Female vervet monkeys (*Chlorocebus aethiops*) remain in their natal group throughout life. When calls from females from groups who had been neighbours all their lives were broadcast, the target individuals reacted more strongly when the playback suggested the caller had transferred group (Cheney and Seyfarth, 1982b). (It is not clear why monkeys should be interested in the demography of social groups that they will never enter, but the data suggests they are.)

Vervet monkey mothers, hearing the cry of an infant, are not only more reactive towards their own infant's cry, but when they are played the calls of other infants they look towards the real mother, showing they recognize mother-infant relationships (Cheney and Seyfarth, 1980). Using match-to-sample, this result was confirmed in captivity for long-tailed monkeys (*Macaca fascicularis*), and extended to the sibling relationship (Dasser, 1988), showing that at least two sorts of kin relationship are distinguished. Moreover, after losing in conflict, monkeys of several species 'redirect' their aggression towards weaker individuals, but specifically towards relatives of the individual who defeated them (Cheney and Seyfarth, 1989; Judge, 1982), showing further awareness of kin relationships. (It is not suggested, of course, that these primates have an understanding of genetical kinship anything like that of humans.)

Some Old World monkey species give specific greeting calls to dominants and subordinates. When target vervet monkeys hear playbacks, their reaction depends on the rank relationship between themselves and the caller. When the caller is dominant to themselves, and gives a 'call to dominant', their agitated reaction suggests they expect a high ranking individual nearby; whereas if the same monkey gives a 'call to subordinate', or a monkey subordinate to themselves gives a 'call to dominant', they give little reaction: they understand the ranks of third-parties relative to each other (Cheney and Seyfarth, 1982a). Playback can even be used to simulate interactions between third parties: when baboons (*Papio ursinus*) hear sounds that suggest a rank reversal in the dominance hierarchy, they react with surprise, specifically if the reversal suggests that the normally-stable rank relationships between matrilineal families have changed (Bergman et al., 2003). Baboons evidently 'eavesdrop' on social relationships: when playback simulated a consorting pair moving apart, which would normally signal a mating opportunity, other

males were quick to head for the 'female' (Crockford et al., 2007). Thus it seems that some non-human primates are able to categorize rank relationships in very much the same ways as do the humans who study them, showing knowledge of relationships among third-parties and not just with respect to themselves, and of the likely degree of stability of rank relationships.

The significance of these findings, from a cognitive perspective, is the implication they have for memory. If an animal distinguishes its social companions and immediate neighbours as individuals, and knows where each ranks in comparison with others, and which other individuals stand in some sort of kin relationship to it, then the memory load increases *exponentially* with group size. In contrast, if an individual reacts to most conspecifics merely on the basis of their appearance and demeanour, as may generally be the case in many socially monogamous birds and herd species, then memory load is *independent* of group size; and if it reacts on the basis only of a dyadic relationship with itself, such as the dominance relationship from recent encounters, then memory load increases only *linearly*. Although primate-like sociality is infrequent among other mammals, some species of carnivore, equines, certain dolphin and whale species and all species of elephant live in groups where they are part of a semi-permanent network rather than an amorphous herd. Social knowledge has yet to be explored in most of these taxa, but work has already begun. Most strikingly, using playback of vocalizations, African elephants (*Loxodonta africana*) have been shown to distinguish at least 80 individuals as familiar, compared to those less-familiar to them in the much larger social network (McComb et al., 2000). It is not known how much information they remember about each of these individuals, or even whether they are all recognized as such. However, in the same population, elephants have been shown to recognize as individuals, and keep

track of among their travelling party, at least 17 female family members based on olfactory cues found in urine (Bates et al., 2008b), and it is therefore entirely possible that elephant knowledge of familiar conspecifics is as deep as that of primates, but over a much larger number of individuals.

Social tactics

As well as good evidence that primates recognise individuals, kinship, rank, and the third party relationships between others, there is now extensive evidence that many species of primate regularly deploy subtle or manipulative social tactics during intra-group competition with these individuals.

While dominance rank is just as important for a primate as it is for other social animals, rank is less likely to be a function of physical power, often deriving instead from the support of third parties (and this is not unique to primates: e.g. zebras: Schilder, 1990). In female-resident monkeys like macaques, the mother may support her offspring against others ranking below her, and in particular her youngest offspring: the result is that offspring attain dominance ranks just below that of their mother, with the youngest the highest ranked (Sade, 1967). In all Old World monkeys, grooming is used to build up alliances, that accrue future benefits in other currencies (Dunbar, 1991), varying the exchange rate in a 'biological market' (Fruteau et al., 2009). Long-lasting social bonds 'pay' in reproductive terms: the offspring of baboons that form strong social bonds with other females live longer, independently of health differences between the parents, and the effects persisted into offspring adulthood (Silk et al., 2009).

Monkeys are selective in whom they choose to form alliances with, targeting their grooming and other affiliative interactions specifically at the most useful allies, such as

those who are dominant or who offer other benefits (Cheney, 1978; Harcourt, 1992). The same specificity in allocation of grooming to the most useful allies has recently been found in meerkats (Kutsukake and Clutton-Brock, 2010), and is perhaps likely in all social species that show allogrooming. Vervet monkeys are more responsive to the (experimentally played back) vocal signals of individuals who have recently groomed them, provided they are not close kin, in which case their responsiveness is always high (Seyfarth and Cheney, 1984). When their most important alliances are disrupted by competition, apes and monkeys of many species make efforts to reconcile afterwards: they are more likely to initiate grooming with a recent opponent than expected from control observations (Cheney and Seyfarth, 1989; Cords, 1992; de Waal and van Roosmalen, 1979; de Waal and Aureli, 1996; Kappeler, 1993). In baboons, vocalizations can be used effectively to reconcile with former opponents, at a distance (Cheney et al., 1995); and even a friendly grunt given by the close kin of a recent opponent serves to reconcile recent aggressors (Wittig et al., 2007b). Likewise, support in aggressive contests can effectively be given by vocalization, creating a ‘vocal alliance’ (Wittig et al., 2007a), and baboons can infer the target of a vocalization from the context (Engh et al., 2006). Nurturing and repairing alliances among non-kin suggests that primates in some way understand that grooming, perhaps as an honest indicator of time invested (Dunbar, 1992b), can be traded in the expectation of future benefits—a form of reciprocal altruism (Trivers, 1971). (Interestingly, in general, evidence for reciprocal altruism among any non-human animals, including primates, is sparse and insecure: Clutton-Brock, 2009). One of the most intriguing ways in which primates manipulate their companions is shown in ‘policing’, found in some macaque species, where a powerful individual intervenes to break up fights among subordinates (de Waal, 1989): the costs of policing falls only on

the intervener but the benefits accrue to all, making policing relatively unlikely to evolve (Flack et al., 2005). Flack and her collaborators have used the technique of ‘knocking out’ particular individuals in a large group of pig-tailed macaques (*Macaca nemestrina*) to investigate experimentally whether policing is effective, finding that infrequent policing by a few powerful individuals significantly preserves the stability of social networks in the face of perturbations (Flack et al., 2006). Whether this form of ‘niche construction’ (Odling-Smee et al., 2003) is based on innate tendencies in pig-tailed macaques or some understanding of the social mechanisms is unknown.

In contrast to cooperation based on temporary coalitions, seen in defence against predators or competing groups of conspecifics, or cooperative breeding systems such as those of callitrichid primates (Burkhart and Van Schaik, 2010), evidence for other forms of cooperation is more controversial. Cooperative hunting in wild chimpanzees (*Pan troglodytes*) has long been described (Teleki, 1973), but although the converging chimpanzees must seem cooperative to the out-manoeuvred prey individual, it is also possible that each chimpanzee follows its individually best strategy (Busse, 1976). A strong case for more than this has been made in the case of Tai chimpanzees of Ivory Coast, a population known for high levels of hunting: coordinated and distinctive individual roles have been described, including ‘driver’ and ‘ambusher’ (Boesch, 1994). Yet at Ngogo, Uganda, a study site where hunting is even more prevalent and similarly appears cooperative, the researchers were unable to be sure that more than individual selfish tactics were involved (Watts and Mitani, 2002). Cooperative hunting is routine in many social carnivores (e.g. spotted hyaenas *Crocuta crocuta*, some populations of lions *Panthera leo* and wolves *Canis lupus*: Grinnell et al., 1995; Holekamp, 2006; Mech, 1970; Stander, 1992) and at least one bird, the Harris’s hawk (*Parabuteo unicinctus*; Bednarz,

1988). Although Stander describes female lions taking account of the movements of others during hunts, the extent to which cooperation is based on any understanding of the strategies of others is usually unknown. An elegant exception is the work of Drea and Carter (2009) who presented pairs of spotted hyaenas with a rope-pulling task that could only be solved by cooperation. They found that hyaenas cooperated quickly and repeatedly, but also improved over time as individuals increasingly took account of the actions of the other, and showed accommodation towards a naïve partner.

Captive studies show that, in principle, chimpanzees should be able to engineer cooperation, since they are able to understand another's role in a two-role task, in which one player is able to see which of several handles will result in food reward for both participants, but only the other player can reach the handles (Povinelli et al., 1992a). In the same task, rhesus monkeys (*Macaca mulatta*) were able to learn either role—but when roles were switched, the monkeys had to re-learn the task from scratch, showing that, unlike chimpanzees, they had no real understanding of the cooperation involved (Povinelli et al., 1992b). When confronted with a task that requires cooperation, chimpanzees may need to learn how to recruit another individual to help (Hirata, 2007), but when proficient they select individuals to recruit who have previously been the most effective collaborators (Melis et al., 2006a). Whether chimpanzees do cooperate or not has been found to depend on the degree of social tolerance between the individuals (Melis et al., 2006b), and their higher general level of social tolerance allows captive bonobos (*Pan paniscus*)—sometimes called the pygmy chimpanzee, and a species not described to cooperate in the wild—to out-perform chimpanzees in cooperative tasks (Hare et al., 2007). Although in general monkeys have failed to give evidence of cooperative abilities, cotton-top tamarins (*Saguinus oedipus*), a cooperatively breeding

species, not only performed well in a two-role task but showed similar capacities to chimpanzees in understanding the role of the other (Cronin et al., 2005). These studies suggest that temperament may be more important than cognitive architecture in whether or not a species is able to cooperate efficiently.

Tactics of social manipulation that rely on deception for their effect are well documented in many species of primate (Byrne and Whiten, 1990; Mitchell and Thompson, 1986). In most cases, there is little reason to think the subjects themselves understand the act of deception—that is, creating a false belief in the deceived individual—and the data can instead be understood as a result of rapid learning in social circumstances, with no insight into how they work (Byrne, 1997b). However, there are a number of cases of deception, specifically in the great apes, which are very hard to explain in this way, and some understanding of mental states becomes a more plausible explanation (Byrne and Whiten, 1992). In corvine birds, too, deliberate deception has been described in the context of hiding or ‘caching’ surplus food, found in several species. Scrub jays (*Aphelocoma californica*) react to others’ seeing them cache their food, by re-caching it once they get the chance, in private—but only if they themselves have prior experience of pilfering the caches of others (Emery and Clayton, 2001). When hiding food items, jays prefer locations behind barriers or in shady locations. Ravens (*Corvus corax*) also take close account of who might have seen them make caches, and among other strategies may make ‘false caches’ of non-existent or trivial items when competitors are watching, delaying their approach to a cache if competitors are nearby, and searching at false sites until the competitor has left (Bugnyar and Kotryschal, 2004). We shall return to the cognitive implications of deliberate deception, below.

Perceiving others

Many species of animal are known to distinguish a range of conspecific displays and body postures, including facial expressions; the greater the degree of control of facial musculature, the larger the number of facial expressions which may need to be recognized. However, displays and expressions are to a large extent under the control of the signaller, and what information it wishes to share: it would be of great utility, therefore, if the involuntary or inevitable movements of the eyes, head and body that show the gaze direction and (presumably) the focus of an individual's visual attention could also be read. Consequently, much effort has been devoted to understanding primate abilities at gaze-following and reading the attention of others.

Gaze following is known in many species of animal (e.g. great apes Brauer et al., 2005; goats, Kaminski et al., 2005; ravens, Bugnyar et al., 2004; ibises, *Geronticus eremita* Loretto et al., 2010), and is often taken to be an automatic, almost reflexive tendency. However, research on monkeys has found gaze following to depend on the particular facial expression of the model (Goossens et al., 2008), and that the ability to accurately follow gaze develops between infancy and adulthood (Ferrari et al., 2008); neither finding is consistent with the interpretation as a reflex. Moreover, in some species, gaze following is 'smart'—that is, subjects are able to follow gaze geometrically. Analysis of collated records of primate deception suggested that Old World monkeys and apes are able to represent the geometric perspective of other individuals (Whiten and Byrne, 1988), although this was later disputed for monkeys (Kummer and Cords, 1991). Subsequently, the ability to follow gaze geometrically, looking 'behind' barriers that occlude the view from their own perspective, has been shown in several species (chimpanzees, Tomasello et al., 1999; spider monkeys, *Ateles geoffroyi* Amici et al., 2009; ravens, Bugnyar et al., 2004);

but not ibises, Loretto et al., 2010. In the wild, bee-eaters (*Merops orientalis*) have been found able to take the perspective of their predators, showing one obvious benefit to the ability to follow gaze geometrically (Watve et al., 2002).

It would seem obvious that gaze following also *indicates* particular places, objects or activities that are the focus of others' attention. Oddly, it has been surprisingly difficult to show that species gain useful information of this kind from gaze-following: for instance in finding food in an object-choice experiment: domestic dogs far outperform chimpanzees (Brauer et al., 2006; but see Krachun and Call, 2009). (Hand-reared wolves do not follow human gaze, apparently because they tend to avoid looking at faces so are unable to learn the significance of gaze direction: Miklosi et al., 2003). Even monkeys, able to use human pointing and other communicative cues, and to follow gaze, do not seem able to use gaze as a cue (Hauser et al., 2007). Recently, however, object choice on the basis of gaze following has been shown in lemurs *Eulemur* spp. (Ruiz et al., 2009), although not at high levels of success. Ruiz et al suggest that their results may not reflect a mentalistic understanding of what gaze means, but rather lemurs are equipped with two useful tendencies: gaze-following, in which gaze is traced to its end point (perhaps geometrically); and gaze-cueing, in which the objects at that point are investigated preferentially. With such tendencies, lemurs gain the benefit of having their attention drawn to useful objects and places, without perhaps understanding anything about what is in the mind of the individual whose attention they follow. We take it that other primate species will prove to have similar capacities, when analyses focus on the lower levels of success in object choice that they allow. (Ravens, whose performance is very like that of chimpanzees, have been shown able to use gaze for object choice with only small modifications of procedure: Schloegl et al., 2008a, b) Whether higher rates of success in

using gaze to choose objects, as shown for instance in dogs, needs any more mentalistic interpretation is not known.

Understanding of the perceptual significance of another individual's perspective has been much more readily shown in gestural communication. Great apes are sensitive to the ability of their audience to perceive gestures, choosing tactile or auditory modality when the target audience is not looking, and silent visual gestures only when they are (chimpanzees, Tomasello and Call, 2007; Tomasello et al., 1994; bonobos, Pika, 2007a; gorillas *Gorilla gorilla*, Genty et al., 2009; Pika, 2007b; orangutans *Pongo* spp., Liebal, 2007; Liebal et al., 2006). Moreover, some individual apes have shown that they understand the utility of concealing embarrassingly revealing signals, such as a chimpanzee who was once noticed to hide his penile erection from a dominant male until it subsided (de Waal, 1982), or a gorilla who regularly hid his play face in order to surprise a play partner (Tanner and Byrne, 1993). The interpretation of these data shades into issues of understanding of the other's thoughts, discussed below.

In the great apes, there is evidence for 'triadic' interactions, in which two individuals interact both with each other and with an object, paying attention to the nature of the other's interaction with the object (bonobos, playing with humans, Pika and Zuberbuhler, 2008; gorillas, playing with each other, Tanner and Byrne, 2010). The apes encouraged reluctant partners back into the game, and moderated their own abilities to continue the game as collaboration, in striking contrast to their normal competitiveness over food items.

As with gaze following, shared attention to objects and the 'intersubjectivity' shown in triadic interactions over objects have been suggested to be important developmental precursors to theory of mind in humans (Trevvarthen, 1977, 1980). One

theory of why non-human primates do not develop further along this route is that they lack the ability to make use of ostension, whereas the human infant is equipped to receive and use this 'natural pedagogy' (Csibra and Gergely, 2009) and is thus much better able to profit from human demonstrations. The general lack of pedagogical teaching among all non-human primates supports this conjecture. Functionally-defined teaching has been recorded in several species of animal, including ants, babblers, meerkats, cheetahs and several callitrichid primates (Caro and Hauser, 1992; Thornton and Raihani, 2008). But none of these data suggest that the teacher understands the (lack of) knowledge of the learner; in contrast, observations suggesting deliberate pedagogy are very rare (chimpanzees, Boesch, 1991; killer whales *Orcinus orca*, Guinet and Bouvier, 1995), and consequently hard to interpret. However, other evidence does not support the uniqueness of human ostension. Whole-hand pointing is used and understood by chimpanzees (Leavens and Hopkins, 1996, 1999), and free-ranging rhesus monkeys have been found to follow a range of human communicative gestures, including pointing and head-indications after eye-contact was established, using them to locate hidden food (Hauser et al., 2007).

Predicting and understanding the actions of others

The ability to predict what others are likely to do next can be critical for survival. It is evident that a wide range of animals are well able to extrapolate the current behaviour of conspecifics, predators or prey, to anticipate what their next actions might be; but the evidence that they may also do this on the basis of understanding (representing unobservable causal factors) is more difficult to obtain.

In the case of social cognition, a key distinction for people is between accidental and intentional action, and whether non-human primates feel similarly has been investigated in various ways. A captive chimpanzee, when a person ‘accidentally’ spilled its prized orange drink and gave it nothing, subsequently continued to beg from that person; but if the loss appeared deliberate, with the juice just poured away, the chimpanzee avoided that person in future (Povinelli, 1991). However, it is difficult to disentangle the influence of emotion from knowledge in such a dyadic interaction, and when strict controls for demeanour were made the effect disappeared (Povinelli et al., 1998; see also Call et al., 2004). To avoid this problem, chimpanzees, orangutans and children were trained on a simple task, where the rewarded choice was cued by previously placing a mark over the site; when additional, apparently ‘accidental’ cues were also dropped in conflicting sites, all three species responded the same way (Call and Tomasello, 1998). At first, the accidental cues were just ignored, showing clear understanding of the distinction; when the ‘accidental’ marking continued both apes and children began to investigate, choosing them instead—but, gaining no rewards, they later returned to following only the deliberately-placed cues.

The signals that indicated intention in the experiments discussed so far are normal everyday actions for the humans whose behaviour the animals had to interpret; thus it is possible that the subjects had been able to learn that such signals carried meaning from their past experience alone. What happens when a wholly new gesture is employed? Humans are able to relate the form of a gesture to the constraints of the environment: if one’s hands are full, one can ‘point’ with an elbow or foot and be readily understood. Non-human primates show the same flexibility, with identical results in cotton-top tamarins, rhesus monkeys and chimpanzees (Wood and Hauser, 2008). When an

experimenter, carrying a large object, touched one of two food wells with his elbow, the subjects responded just as if he had used his hand normally, preferentially investigating that place (Wood and Hauser, 2008). But when the same experimenter used his elbow, in the same way but with his hands not engaged, the gesture was ignored, just as was a hand-touch that looked unintentional. A similar ability, to differentiate the relevance of an action from its situational context, has been noted when preverbal infants copy actions (Gergely et al., 2002). When a switch is pushed with the experimenter's head, the infant only copies that detail if the model's hands are free; if he is holding a cloak, then the infant simply uses her hand: this has been described as 'rational imitation'. Modifications of this paradigm have been used with chimpanzees that have been reared with humans, and with domestic dogs; in both cases, the subjects showed 'rational' selectivity of what to imitate (Buttleman et al., 2007; Range et al., 2007).

Understanding of another's thoughts

Often treated as the cognitive Rubicon between humans and other animals, the suite of abilities that ultimately allows us to interpret other people's actions in an intentional way as a consequence of their desires, knowledge and beliefs, has been subject to immense research activity over the 30-odd years since Premack and Woodruff first asked, "Does the chimpanzee have a theory of mind?" (Call and Tomasello, 2008; Premack and Woodruff, 1978). We can give here only a sparse summary of this literature for non-human primates.

Throughout the period, there has been something of a gulf between the conclusions of observers of natural primate behaviour, and those who carry out controlled laboratory studies (de Waal, 1991). Of course, it is easy to over-interpret the

richness of observations, and experiments may fail for many reasons other than cognitive limitations of the subjects, so some gap is to be expected—but in this case, more seems to be going on. In particular, analysis of primate behavioural deception based on observational data concluded that, although most records could well reflect no more than rapid learning in social contexts, some did imply more (Byrne and Whiten, 1985; Byrne and Whiten, 1992; Whiten and Byrne, 1988; for chimpanzees, specifically, see also de Waal, 1982, 1986). Evidence was noted that great apes of all species seemed to represent the ignorance, knowledge and false belief of other individuals. This proposal has been the subject of much dispute and many empirical studies.

An early paradigm for investigating whether animals understand the difference between knowledge and ignorance and realize the connection between seeing and knowledge has been called the ‘guesser/knower’ design (Povinelli et al., 1990). In it, the subject is confronted with conflicting hints as to which of several sites has been baited: from one individual who was clearly present at and able to see the baiting, the knower, and one who was not, the guesser. Initial reports that chimpanzees could solve this puzzle, whereas rhesus monkeys could not (Povinelli et al., 1991), were challenged because experiments gave differential reward during testing, and thus rapid learning might simulate understanding (Heyes, 1993). Careful re-analysis showed this to be very possible (Povinelli, 1994). A subsequent study with domestic pigs, using a design that avoided rewarded test trials and used conspecifics as informants rather than humans, identified one pig that apparently understood the seeing/knowing connection, although other subjects’ data were ambiguous (Held et al., 2001). Extensive work with chimpanzees, using a simpler paradigm in which the subject must beg for food from an experimenter who may or may not be able to see them, concluded that the chimpanzee

has no general understanding of the relationship between seeing and knowing (Povinelli et al., 2000; Povinelli and Eddy, 1996; Povinelli et al., 1994).

One possible problem with these designs is that they depend on the subjects taking cues from helpful onlookers, or expecting help from others: chimpanzees and indeed most non-human primates may have little natural experience with such cooperative interactions (Hare and Tomasello, 2004). Suspecting that this might have been the problem, Hare and co-workers designed a competitive perspective-taking task, in which the subject must assess what its (dominant) competitor has been able to see of foods that may be hidden by visual barriers, and avoid competing for food that it knows about (Hare et al., 2000). With this design, chimpanzees clearly showed that they were well able to compute what a competitor had seen from witnessing the situation from its own perspective, confirming the evidence for geometric perspective taking discussed already. Moreover, when the competitor was swapped for another equally dominant individual, mid-experiment, the subjects took account of the lack of prior exposure of the newcomer: they were apparently able to represent what others had *previously* seen, in other words what they know, as well as what they can currently see (Hare et al., 2001).

Although some still dispute this interpretation (Karin-D'Arcy and Povinelli, 2002; Povinelli and Vonk, 2003), considerable converging evidence now supports the contention that chimpanzees can appreciate the knowledge versus ignorance of other individuals (Call and Tomasello, 2008; Tomasello et al., 2003). When tested in a competitive situation, rhesus monkeys also show understanding of the visual perspective of others: where they could steal a grape from one of two humans, they reliably chose the person who was unable to see their action (Flombaum and Santos, 2005). Similarly, monkeys evidently understand the connection between hearing and knowing, preferring

to take food from 'quiet' containers that will not alert an inattentive competitor to their theft (Santos et al., 2006). Experimental study of caching in scrub jays suggests, in this corvine bird, understanding of knowledge similar to that found in chimpanzees. If two (jay) competitors have seen a jay cache different items in different places, the jay remembers who has seen what, and takes measures appropriately when confronted with one or the other competitor (Dally et al., 2006).

It is much less clear whether any non-human species understands the concept of false belief: part of the problem is that experiments with non-verbal subjects can easily become very complex, which itself may make for failure. Kaminski and colleagues attempted to tackle this question by using a competitive game between two individuals, either children or chimpanzees, in which the subject could make only one choice in each trial: they could opt for turning over one of three cups, having seen a high-quality food item placed under one of them, or choose a low-quality reward instead (Kaminski et al., 2008). The two subjects took it in turn to choose first, and the second could not see what the first had chosen: the high-quality item might already have been taken by then. Indeed, when they had seen a cup baited with a high quality food, and also seen that the other saw the same baiting process, both 6-year old children and chimpanzees wisely avoided that choice when it was their turn. Both species therefore showed differentiation between knowledge and ignorance. In a second experiment, the experimenter picked up the food after the baiting process, and either put it back or moved it to a new location: conditions differed in whether both subjects, or only the second to choose, saw this extra move. In the latter instance, the smart strategy is to go for the high-quality food, since the first subject should have falsely believed that the food was elsewhere and wasted their turn. Six year old children, but not 3 year olds, used this strategy, showing that the task was not

too complicated for older children to use their understanding of false beliefs in its solution. The chimpanzees did not. However, other work suggests that babies much younger than 3 years can represent false beliefs (Onishi and Baillargeon, 2005; Southgate et al., 2007), so the failure of the 3 year old children—and thus also of the chimpanzees—in Kaminski et al's task may after all reflect confusion from the task's complexity.

Rather similar findings were obtained with free-ranging rhesus monkeys, using a simpler design (Santos et al., 2007). Santos and colleagues used an expectancy-violation experiment, using looking-time as an indication of surprise, based on the task originally devised for human infants (Onishi and Baillargeon, 2005). Subjects were presented with a stage on which a plastic lemon was able to move on a track, from side to side: in the critical trials, the human presenter was apparently unable to see some of the movements of the lemon because of an occluder, although the monkey could. Thus, if the occluder was absent and the presenter watched closely while the lemon moved to a new location, they should have a true belief of its position; but if the occluder blocked their view during the same move, they should have a false belief (out of date information) about the current position. When monkeys watched the presenter's subsequent search for the lemon, their looking times showed they expected the presenter to search in the right location in the true belief condition, and were surprised (longer looking time) if they searched elsewhere. However, in the false belief condition, looking times did not differ: monkeys, unlike human infants, appeared not to have any expectations in this case (Santos et al., 2007). Perhaps the only animal able to compute the consequences of a false belief in another is the human; but the deceptive behaviour of corvids and great apes is in conflict with that conjecture, and resolution is needed.

Understanding the self

Against the background we have so far sketched of impressive abilities in perceiving, recognising, understanding and interpreting other individuals, one *failing* is striking in animals: the failure to recognize the subject's own face in a mirror. Of course, individuals of any species would need experience to grasp the true origin of the realistic moving image they see in a mirror—even humans, as first contacts with New Guinea highlanders showed repeatedly in the last century. But animals that live as human pets, or that are given months to explore a fixed mirror in a zoo cage, have ample opportunities: to touch its surface; to notice the match between the fingers/paws/hooves/etc. visible in and on the mirror; to observe parts of their own body and those of other individuals, both directly and in the mirror, moving in step. Nevertheless, the great majority of animals persist in giving 'social' responses, as if the image were another individual not themselves, or learn only to avoid looking at the mirror. Even monkeys, many species of which have been tested with the classic 'mark test' (Gallup, 1970), where a surreptitious mark is placed on a part of the head which the animal cannot see, completely fail to give any evidence they realize the face in the mirror is their own (Parker et al., 1994). (And other paradigms that have been claimed to show self-recognition in monkeys remain highly controversial: Anderson and Gallup Jr., 1997; Hauser et al., 1995). It is not that monkeys cannot understand the geometric transformation produced by a mirror, because they readily learn to use a mirror to guide out-of-sight actions (Anderson, 1984). But those species that recognize themselves in mirrors are the exceptions.

All species of great ape *do* recognize themselves in mirrors (Parker et al., 1994; Povinelli et al., 1993), although not every individual of any of them (Mitchell, 1996;

Swartz and Evans, 1991). Similar evidence of self-recognition, including appropriate responses in the mark test, has been found in a corvine bird, the magpie *Pica pica* (Prior et al., 2008). In addition, both bottlenose dolphins (*Tursiops truncatus*) and gibbons (*Hylobates* spp.) have given indications that they understand their mirror images, such as mirror-contingent movements and use of the mirror to inspect parts of their body (Hyatt, 1998; Reiss and Marino, 2001; Ujhelyi et al., 2000); it is difficult to see how dolphins could do much more to convince, whereas gibbons have repeatedly failed the mark test (Suddendorf and Collier-Baker, 2009). Asian elephants (*Elaphus maximus*) have been tested for mirror self-recognition several times, with mixed results (Plotnik et al., 2006; Povinelli, 1989; Simonet, 2000). Plotnik and colleagues report one elephant that responded quite differently when it had been surreptitiously marked with a visible spot, and did not do so when sham-marked invisibly, suggesting self-recognition; however, these responses were not immediate on catching sight of its mirror image, as is seen in the case of great apes, nor particularly performed in front of the mirror.

In trying to understand what prevents most species accomplishing what appears to be a simple matching task—and therefore what is special about humans and other great apes, magpies and probably dolphins and elephants—it may help to consider another ‘strangely lacking’ sign of understanding: that of death. Whereas humans are highly disturbed by the death of a close companion, and usually show some sort of mourning, most animals do not. Farmed red deer (*Cervus elaphus*), for instance, give no reaction when one of their daily companions is shot through the head and falls dead as they feed around it (John Fletcher, *pers comm.*): they are habituated to the sound of a gun, and no distress signals are given by the deer because it dies instantly. Stillborn infants are often carried or groomed by their mothers, in monkeys and especially great apes, and also

sometimes by carnivores like leopard (*Panthera pardus*); but it is difficult to interpret these isolated observations. The behaviour of African elephants, then, stands out, because they show a special interest in the bodies of their kind, as well as showing empathic and helpful reactions towards distressed or dying individuals (Douglas-Hamilton et al., 2006); these behaviours are directed towards both kin and non-kin. Experimentally, stronger reactions of curiosity and exploration were shown to elephant bones and tusks (washed clean of scent with detergent) compared with similar-sized bones of other species (McComb et al., 2006). While the elephant graveyard is a hoary myth, elephants do seem to show strong and unusual reactions to the death of a conspecific compared to most species. The recent description of the death of a chimpanzee within a cohesive and long-established social group strongly suggested that this species, too, has some understanding of death (Anderson et al., 2010): pre-death care, inspection of the body for signs of life, night-time attendance at the corpse by relatives, and later avoidance of the site of death.

Since individuals of almost every social species will have opportunities to observe conspecific death and its consequences, the real mystery is why such reactions are so rare. One possibility is that, without a representation of the self as an entity, the death of others has no personal significance, unless one is immediately dependent on their aid. Similarly, without a mental representation of the self as independent entity, it may be impossible to understand the face staring back from the mirror. If so, then those species likely to react with understanding to the death of others should be specifically those showing self-recognition (as suggested by Gallup, 1979). This hypothesis could be tested by further research on reactions to conspecific death, concentrating on species well-known to be able or unable to recognise themselves in a mirror. Reactions to the death of companions and recognition of the self are phenomena that may also relate to a general

capacity for empathy, which has similarly been identified in the great apes (de Waal, 2009; de Waal, 2008) and in elephants (Bates et al., 2008a).

What underlies primate social sophistication?

As this brief review has demonstrated, social sophistication is by no means unique to primates, nor is it uniform within non-human primate species. Unfortunately, comparable work on many other species is still in its infancy compared to that on primates, so there is no ‘level playing field’ of comparison. Based on the evidence currently available, however, we shall distinguish between social complexity that is a matter of degree—knowledge of *more* social companions, *more frequent* use of alliances, *more complicated* manipulative tactics that depend on picking more subtle aspects of behaviour, finer and *more elaborate* categorizations, *larger brain* (part) sizes that correlate with larger social groups—from social complexity that requires a deeper understanding of mechanism and mind, including the understanding of the self as an entity, and perhaps of the false beliefs of others, which is apparently very much more limited. In the case of great apes, there is some evidence for both these features. In other taxa, it may be that either type of social sophistication can occur without the other—for instance, social carnivores apparently show quantitative social complexity, whereas some corvids give evidence of deeper understanding—so the selective pressures that led to their evolution may be different in kind. We shall examine the pattern of species differences in social sophistication, using the comparative method, for evidence of their evolutionary origins, and assess whether these ‘two types of intelligence’ derived from the same or different selection pressures. Then, we shall return to the issue of what cognitive mechanisms might underlie the social competence seen in animals.

Evolution of species differences in intellectual ability

Theories of what led ultimately to human intelligence abound; but to assess them it is critical that the pattern of abilities among living primates and other relevant species be properly characterized. Use of brain size (or neocortex size, executive brain size etc.), appropriately scaled against the rest of the brain, as a proxy for intelligence has shown increases with group or clique size in all groups of primates (Barton and Dunbar, 1997; Barton and Harvey, 2000; Dunbar, 1992a, 1998), giving strength to Humphrey and Jolly's earlier suggestions that social complexity selects for intellectual increase (Humphrey, 1976; Jolly, 1966). (Scaling against body size is inappropriate for estimating the intellectual potential of a given brain size, although it has often been used for that purpose. Instead, it is useful as a measure of the brain's 'cost' to the animal: Byrne, 1996). Comparing with data from other mammals gives support to social complexity as the forcing function that leads to quantitative increases in social skills. Similar correlations to those found in primates, between neocortex enlargement and social group size, have been found in carnivores, insectivores and bats (Barton et al., 1995; Dunbar and Bever, 1998). In even-toed ungulates, none of whose cognitive abilities seem to rival those of primates, there is no similar relationship between brain size and group size (Shultz and Dunbar, 2007), presumably because individual recognition and social differentiation is not a feature of these groups. However, among birds, where the common association pattern is social monogamy, and no group size effects have been found, ape-like abilities have been discovered in corvids (ravens, scrub-jays, magpies); this evidently cannot be explained in the same way (Emery et al., 2007). This strongly supports the speculation that two different evolutionary pressures have effected change in animal intelligence.

If, at least among mammals, living in a semi-permanent social group presents a particularly acute intellectual challenge (Byrne and Bates, 2007), what are the key aspects of that challenge? Two main suggestions have been made:

(a) Arms-race: social competition within the group may favour those with greatest social ability, and hence brain size, but in the next generation the population averages will have increased, giving a runaway arms-race (Humphrey, 1976). But the tendency to create an arms-race would seem to be shared with other theories: for instance, social competition by means of skilful interaction with the environment, promoting increased physical cognition; and interactions with food competitors, predators or prey. (And in the latter case, the evolutionary pressure is greater as the stakes are higher.) Also, in general, kin relationships within primate groups might be expected to reduce the benefits of any individual competition within the group.

(b) Unpredictability: whereas the environment may be complex but is ultimately predictable, social interactions with similarly-intelligent, behaving agents will always remain more difficult (Barton, 2006). But, again, predator/prey interaction is surely just as unpredictable, and finally more critical as lives are at stake.

Fossil evidence supports the conjecture that predator-prey interactions are a powerful selection factor for intelligence, with arms-races between predators and prey evident in the step-by-step increases in brain size of both, co-evolving in the same continent (Jerison, 1973), and reduction of brain size in island species lacking predators, compared to their relatives and ancestors in continental habitats (Byrne and Bates, 2007). As a resolution of this issue, we suggest that *all* competition that is based on knowledge of the behaviour of animate entities should be seen as affecting ‘social’ cognition (Byrne

and Bates, 2007); continual unpredictability is found, and arms races are set in train, whether the challenge is dealing with predators or companions.

However, it may be that the focus on social cognition by researchers has eclipsed more general cognitive differences: if so, social competence might be a side-effect of some other, external factor; or selection for social skill might give side-benefits in other areas. Critical to this debate is whether primates are specialized in social intelligence but remain primitive in their representation of the physical environment, or show advanced intelligence in *any* domain that is tested. The debate is an old one also in human intelligence: the question of single-factor (*g*) versus multiple intelligences has been long-discussed, and time has brought no clear resolution. The case for modular social intelligence in monkeys was made by Cheney and Seyfarth (1985, 1990), but a recent meta-analysis of an extensive range of laboratory tests of primate ability supports single-factor intelligence in primates (Deaner et al., 2006). Under natural conditions too, there is evidence in favour of a single factor behind differences in species intelligence among primates: a similar relationship has been found with brain size in social skills (deception, Byrne and Corp, 2004; social learning, Reader and Laland, 2001) and physical skills (tool-use and innovation, Reader and Laland, 2001). The forcing function that led to species differences in primate ancestry might therefore have been challenge in either social or physical cognition—or both, at different times in evolution. There is growing evidence for the latter scenario.

Brain-size differences and reliance on sophisticated social manoeuvring are well correlated across primate species in general, and the relationship of brain size to group size provides a strong case that social challenges selected for intellectual advance over a long—60Mya—timescale. As suggested above, ‘social’ should be seen to include

challenges met by information processing in the context of predator/prey interactions, as well as those from living with conspecifics. With this interpretation, linked increases in intelligence and brain size in a much wider range of species may be understood.

But in the great apes, that theory fails: social challenge, as measured by group size, does not differ between ape and monkey species, whereas capacity in some cognitive dimensions—such as understanding cooperation, intention and deception, and mirror self-recognition—do (Byrne, 1997a). Instead, what is notable about apes, *contra* monkeys, is that all genera of living great apes show special skills in manual food processing: *Pongo*, in accessing spiny rattans and palms (Russon, 1998), and for extracting honey and seeds with tools (Fox et al., 1999); *Gorilla*, for processing physically-defended herb resources (Byrne, 2001); *Pan*, in collecting insect foods with tools, often ones made themselves and sometimes sets of two tools for a more complex task (McGrew, 1994; Sanz and Morgan, 2007). Moreover, in captivity all great apes demonstrate remarkably similar tool-using and tool-making abilities, though many populations show no tool-use in the wild (McGrew, 1989), suggesting that the underlying cognitive skills—all ones to do with feeding—have an ancient origin in the common ancestry of all the modern lines. For these reasons, it has been argued that the cognition of the great apes (that is, the qualitative differences from monkeys in their understanding of mechanism and mind) developed over a much shorter timescale, since the living species share common ancestry at about 16 Mya (Byrne, 1997a).

Why should great apes have faced greater challenges in the physical environment than monkeys? They are all larger-bodied, and adapted to brachiation, allowing small-branch feeding but making long range travel inefficient; yet in nearly all habitats they are found today, great apes compete directly with monkeys for ripe fruit and tender leaves.

Old World monkeys are able to digest coarser material than apes, so able to exploit ripening plant food before their competitors. Since monkeys appear to possess all the aces, it becomes a problem to explain why great apes did not become extinct (although many species did, after 14Mya). The suggestion is that the surviving great apes were able to compete by developing skills to reach foods that monkeys could not reach, as shown today in their expertise at extracting insects and dealing with plant defences: abilities that give them advantages in the domain of physical rather than social cognition. The finding in corvid species, few of which are social, of remarkably similar cognitive skills to those of apes similarly points to physical cognition as the driving function for these capacities (Emery and Clayton, 2004, 2009).

An interesting exception to the lack of need for tool use in monkeys is the recent discovery of hammer and anvil use in wild capuchin monkeys (*Cebus libidinosus*) (Fragaszy et al., 2004; Moura and Lee, 2004). The monkeys transport heavy stones to nut-cracking sites, selectively choosing stones of appropriate hardness and size, and of weights appropriate to different kinds of nuts cracked, showing an ability to anticipate their future needs (Greenberg et al., 2009; Visalberghi et al., 2009). This local tradition of nut-cracking is found in several areas of Brasil, but always in arid and inhospitable ones: although capuchin manual skills in no way rival those of great apes, it may be significant that they are similarly brought to their apex by severe feeding challenge.

Increasing evidence suggests that, at least in great apes, the repertoire of cognitive skills in any individual also depends on opportunities for social acquisition of knowledge (van Schaik et al., 1999; van Schaik and Knott, 2001; strong evidence for transmission of social habits has also been found in capuchin monkeys, Perry et al., 2003; Perry and Manson, 2003). ‘Species intelligence’, by analogy with usage of the term intelligence in

differential psychology, refers to the innate potential for cognitive power of every individual of the species; but the extent to which that potential is realized may depend on an individual's social network (Meulman and Van Schaik, 2009). This 'cultural intelligence' view applies most radically to the difference between individuals reared in the wild or captivity: between the bleak circumstances of an old-fashioned zoo and the enriched environment of a human home, or between either and the complex environment of a tropical forest. We expect that among wild populations of some animals (at least, the great apes) the set of cognitive skills in any population will differ, not simply because of the social group size or group complexity, but more specifically on the opportunities for social learning afforded to individuals within the population.

The cognitive basis for differences in social abilities

We have suggested that two accounts are required to explain the differences in cognitive skills observed among primates, as well as some other animals. *Quantitative* differences in social knowledge and social tactics, as seen in several mammalian radiations and in which neocortex size correlates with social group size, need to be distinguished from the *qualitative* differences in understanding, seen in great apes, some corvids and possibly others such as dolphins and elephants.

The quantitative differences are the simpler to explain: as variation in memory abilities (Byrne, 1996a). If neocortical volume affects the ability to record information about identity, association patterns and past histories of behaviour of individuals, then a need to live in socially more challenging settings would be expected to select for increase in neocortex size, underwriting continuous variation in abilities. Correlated increases in

non-social abilities are a by-product of this selective effect, based on the fact that a large and efficient system of perceptual categorization and memory has many other uses.

A bigger problem is to explain the qualitative differences in social understanding, seen in fewer taxa and not associated with social group size. Although no non-human has clearly been shown to represent false belief, the abilities of great apes—and some corvine birds, dolphins and perhaps a few other species—in cooperation, deception, perception of intent, and mirror self-recognition, seem sufficiently distinct from those of monkeys and all other terrestrial mammals to require a different explanation. We develop one possibility here, based on mental representation of behavioural structure, but others are surely possible.

The issue is to what extent innate structure is needed to ground new knowledge—and this is nowhere more acute than in the social domain. Both in primatology and developmental psychology, researchers have shown that statistical regularities can be extracted from complex input information, potentially underwriting remarkable abilities that are often ascribed to more ‘thinking’ processes. Most dramatically, 8-month old infants were found able to segment fluent speech after only 2 min exposure: since the speech was made up of artificially-generated nonsense syllables, only the rules by which the syllables were made up from letter sounds could have allowed this segmentation, showing a powerful innate ability to detect and use statistical regularities (Saffran et al., 1996). Adult humans, shown videos of familiar manual activities reduced to moving patterns of fluorescent dots on limb-joints, were able to segment the activities into phases which corresponded to meaningful subroutines of the overall behavioural program, even though the subjects had no indication what each activity was about (Baldwin et al., 2008). In the non-human primate domain, Byrne (1999, 2003) showed that the ability of great

apes to learn novel structures of skilled action by observation can parsimoniously be accounted for by just such *behaviour parsing* abilities, without requiring prior understanding of the model's purposes or how their behaviour achieved its effect. When a goal-directed manual activity is carried out repeatedly by a skilled practitioner, the activity contains clues in its pattern of statistical variation—the location of pauses, the sections of process which can be omitted or substituted with others, the regularity of sequences of certain steps among the general variation of movements—which allow the underlying 'program-level' structure of action to be discerned. This may account for the differences among animals in imitative learning. For instance, although imitation has often been claimed in primates, most cases can be accounted for rather simply as priming effects, acting upon existing motor skills, rather than involving new learning (Bates and Byrne, in press; Byrne, 2002a; Hoppitt and Laland, 2008). Only in the great apes does it seem that imitation involves learning new skills by assembly of novel actions from components (a recent challenge to the data underlying this statement is based on a misunderstanding of program-level imitation: Byrne et al., in prep; Tennie et al., 2008). This difference implies that only great apes, among primates, have behaviour parsing capacities.

Can this theoretical formulation be extended more generally in the social domain? In principle, it would seem so: just as the behaviour parsing model, in its rather Humean approach to causality, treats *correlations* as causal, so intentions may be treated as those *results* that satisfy an agent that has been seen to be engaged in directed activity (Byrne, 2006). In this way, it should be possible for any animal with a natural ability to parse behaviour to determine the goals of others and relate those goals to the individuals' prior histories, provided they are allowed sufficient experience from which to extract statistical regularities. Admittedly, this allows only a weak understanding of intention, but perhaps

that is all any non-human primate is capable of representing. From an evolutionary point of view, the issue is only whether advantage is conferred over individuals with *no* understanding of intention.

However, without some extra ingredient, this approach would have difficulty in accounting for the differences between species: the failures and inadequacies become the stumbling block for comparative explanation, rather than the successes. On current evidence, only a few species show ‘extra’, qualitatively different social capacities compared to most mammals and birds: why just them? Dealing with this concern may require a more Kantian formulation, in which some crucial mental structure(s) must be innate, and differ qualitatively between taxa, whereas statistical extraction of regularities ‘fills in the gaps’ from practical experience. In an analogy from the physical domain, consider monkeys’ representation of causal properties. Tamarin monkeys are sensitive to the properties of material that are relevant to tool-using, such as rigidity and length, but not colour and texture, despite not being tool-using monkeys (Hauser, 1997). It seems monkeys are predisposed to represent properties that will—in some species, in some environments—permit intelligent tool use to be acquired. But in species that lack an innate predisposition to represent the correct properties of materials, intelligent tool use will never be developed.

What innate mental structure(s) might allow certain animal taxa to develop ‘extra’ capacities in the domain of social behaviour? In principle, ‘structure’ can be provided in two independent ways. The simpler way involves innate heuristics. For instance, a well-known principle in animal learning is that innate ‘constraints’ may focus learning on biologically useful things, determining what is learnt easily and what is not: rats associate nausea but not electric shock with novel foods eaten many hours earlier (Garcia et al.,

1966); perhaps similar genetic channelling determines we so readily learn to fear spiders but have to be strictly taught to fear electricity. At a more general level, the degree of native curiosity and the tendency to latent learning, picking up useful knowledge from certain situations, will be greater in species evolved to fill generalist niches in fast-changing environments. Moreover, species that depend on motor or social skills may be naturally playful during the juvenile period, the play tending to allow development of an augmented motor repertoire and social skills (Bruner, 1972; Caro, 1995; Fagen, 1976; Whiten and Byrne, 1991).

This level of explanation can account for some of the quantitative differences between species, for instance those dependent upon the complexity of social system and fineness of social categorization. When it comes to species differences that imply deeper levels of understanding, it may be necessary to invoke differences in cognitive architecture. For instance, social transmission of information occurs in monkeys and great apes, but the effects are apparently very different, with monkeys unable to learn complex *novel* behaviour by imitation (Byrne, 2002a; Visalberghi and Fragaszy, 2000). Is this because they have different cognitive systems? If species are not able to form the same mental representations, then what they can do with the same information may be radically different (Byrne et al., 2004). For instance, any social vertebrate is likely to benefit from social learning in some way, but those species that code what they see in terms only of a 'conspecific engaged in activity at a place' may only gain from local enhancement (Hoppitt and Laland, 2008). In contrast, if a species is able to code the time-sequence of specific actions applied by that conspecific, what it learns will be much richer (Byrne, 2002b).

We propose that the distribution of behaviour parsing abilities will be critical to species differences, both directly and indirectly. Direct benefits accrue when understanding of others' actions is required to deal with challenges: for instance, when correct interpretation of a social situation requires working out the intention behind another's actions, or in imitatively acquiring a complex skill that would be unlikely to be discovered by trial and error exploration. In order to use the gist of another's behaviour as a structure with which to build novel actions, it will be essential to have, in tandem with the perceptual process of behaviour parsing, the ability to build up hierarchically organized programs of goal-directed action, which will otherwise be evident in general problem solving behaviour: *planning* capabilities. Indirect benefits come from the informational content that can be passed on by social learning and culture, allowing adaptation to local environments to be mediated by social learning as well as genetical evolution (van Schaik et al., 1999; Washburn and Benedict, 1979; Whiten, 2000).

In summary, we suggest that social cognition is not unique to primates, and that primate cognition is not uniquely social. We argue that most demonstrations of cognitive skill can be accounted for by quantitative differences in memory, with the tendency to larger memory most likely being driven by social competition (from conspecifics, and from predator/prey interactions). However, some particular skills such as cooperation, deception, perception of intent, imitation of novel skills, and mirror self recognition, signify a qualitatively different representation of mechanisms and minds. This probably relies on the presence of specific cognitive architecture which allows for behaviour parsing and the formation of hierarchically organised programs of action, the selection for which may have been driven by physical constraints. Our account of behaviour parsing has necessarily been focused narrowly on primates: the evidence is just not there

for other species, including those unusual species that show convergent abilities with great apes. The challenge for future research will be to discover whether this explanation might apply more generally, or whether a wholly new theory of higher-order cognitive abilities will need to be developed to explain the full pattern.

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