

Introduction. Social intelligence: from brain to culture

Humans are perhaps the most social animals. Although some eusocial insects, herd mammals and seabirds live in colonies comprising millions of individuals, no other species lives in such a variety of social groups as *Homo sapiens*. We live in many different sized societies, from small, nomadic hunter-gatherer societies to cities consisting of millions of people living in close proximity; we form special social bonds with kin and many of us make lifelong commitments to one socio-sexual partner, represented in the shape of a marriage.

Although the fledgling concept of social intelligence was formulated over 50 years ago by Chance & Mead (1953), and more explicitly by Jolly 13 years later (1966), it was perhaps Nick Humphrey's (1976) seminal paper on the 'social function of intellect' that paved the way for the past 30 years of productive research in so many seemingly unrelated areas of the biological and social sciences. It is Nick's significant contributions, as evidenced by the number of quotations to his work in this special issue, and the anniversary of the birth of the 'social intelligence hypothesis' (SIH), that were celebrated at a Discussion Meeting of the Royal Society on 22 and 23 May 2006 and which form the basis of this special issue.

Humphrey (1976) argued that the physical problems which primates face in their day-to-day lives, such as finding and extracting food or hunting and evading predators, are not sufficient to explain the differences in intellectual capabilities of animals in laboratory tests. Indeed, many animals with very different levels of cognitive ability have to solve similar kinds of problems in their natural environment. So, why do primates, especially humans, have such large brains? Observations of social groups of gorillas in the field and macaques at the Sub-department of Animal Behaviour, Madingley, led Humphrey to suggest that recognizing, memorizing and processing 'technical' information was not the driving force behind the evolution of primate intelligence. He proposed that it was the intricate social interactions of these animals, their ability to recognize individuals, track their relationships and deceive one another, which occupied their time and substantial brainpower. In particular, it was Humphrey's emphasis on the importance of predicting and manipulating the behaviour and minds of conspecifics which led to the development of 'theory of mind' as a major research focus in both comparative and developmental psychology. The question of whether animals possess a 'theory of mind' occupies

many researchers to this day, and forms a major focus in this special issue in the papers by Barrett *et al.* (2007), Clayton *et al.* (2007), Moll & Tomasello (2007) and Penn & Povinelli (2007).

The first series of papers in this special issue highlights comparative studies on a wider group of animals than have been previously described with respect to the intricacies of social life, including several species of birds as well as mammals. What is perhaps striking about all these papers is the renewed importance of the cognitive mechanisms of prosocial behaviour and social tolerance, particularly cooperation and coordination. Moll & Tomasello (2007) go as far as to propose a new form of social intelligence, the Vygotskian Intelligence Hypothesis, which states that sharing focus on the same events in the environment and directing such focus into mutual cooperation and collaboration is what separates us from other animals. Although not necessarily new, the role of intelligence in the positive side of sociality has tended to be the poor cousin of Machiavellianism, deception and competition as exemplified by Frans de Waal's 'Chimpanzee Politics' (de Waal 1982). It should be stressed that the key to surviving a complex social world is probably the delicate balance between cooperation and competition. Certainly, fostering successful affiliative relationships can lead to the procurement of resources ordinarily unavailable to singletons by joining forces and competing with others. Evidence for this can be found in the alliance formation of male dolphins (Connor 2007) and the pair bonds of rooks and jackdaws (Emery *et al.* 2007). Interestingly, both dolphins and corvids appear to maintain their relationships using mutual contact and behavioural synchrony, a clear case of convergent evolution between distantly related species living in very different environments.

This renewed focus on the nicer side of sociality does not mean that competition, deception and Machiavellianism are no longer seen as playing important roles in social interaction—far from it. The behaviour of western scrub-jays described by Clayton *et al.* (2007) suggests that these food-storing birds are very protective of their caches, particularly against the possibility of pilfering, either when the potential thief is still present, or in the future when the thief has left the scene. These birds implement a number of complex cache protection strategies such as hiding food behind barriers, in the shade or at a distance, move their caches around as a confusion tactic and even protect caches based on the identity of the observer or their knowledge state. Perhaps most interesting from the perspective of human 'theory of mind' is the fact that the jays need to have had experience of stealing another bird's caches

One contribution of 19 to a Discussion Meeting Issue 'Social intelligence: from brain to culture'.

before they can implement these strategies. As birds can play the roles of both cachers and stealers (often at the same time), Clayton *et al.* (2007) suggested that a 'cognitive arms race' can develop, in which cachers develop increasingly sophisticated strategies to protect their caches, therefore pilferers have to develop increasingly sophisticated counter-strategies in order to steal them. The implications of this research for the long-held assumption that big brains are required for developing cognitive strategies and counter-strategies are significant, as scrub-jays have small brains (even though the same relative size as apes). Similar deceptive behaviours are described in the papers by Moll & Tomasello (2007) for great apes, and Reddy (2007) for human children.

The early formulation of the SIH was, not surprisingly, very anthropocentric and primatocentric. Almost nothing was known about the cognitive abilities of non-primates from laboratory tests, and although many animals were studied in the field, including studies of their social behaviour, the focus of those studies was not to understand their intelligence. By contrast, monkeys and apes live in large social groups consisting of many individuals who recognize one another, and who appear to recognize who is affiliated to whom. Social intelligence, therefore, was originally formed to explain how a primate can keep track of multiple relationships, and use this information in a largely competitive framework, such as gaining access to resources. Thus, the quantity of relationships was deemed more important than the quality. A cursory glance to other distantly related taxa, such as birds, reveals that very few species form social groups of the same type as primates. Indeed, the most common social organization of birds is monogamy. Even though these birds form large aggregations during winter foraging before the breeding season, their core sociality is to form pair bonds, which in some species may last their whole lives. Although dolphins do not form pair bonds, their alliances can be very valuable and lead to increased fitness. By contrast, hyenas (Holekamp *et al.* 2007) and cercopithecine monkeys (Barrett *et al.* 2007; Silk 2007) form large, relatively stable matriline groups, which seem to be based on a balance between competition and cooperation. In these species, any bonds which form are either based on relatedness (kin) or are transient and unstable between unrelated individuals. Silk (2007) provides evidence from a number of mammals that fostering these relationships can lead to significant reproductive benefits, including an increased chance of offspring survival. Her paper is perhaps the first to describe in detail why being socially intelligent can be adaptive.

The formation of cohesive social groups also facilitates information transfer in the form of social learning. Although there is good evidence for social information transfer in many animals, and even suggestions of behavioural traditions in isolated populations, there is still little clear evidence for culture in non-human animals. Byrne (2007) suggests that the case for culture may have been overstated and the so-called evidence may be the result of a 'pattern of local ignorance based on environmental constraints on knowledge transmission'. For example, some

populations of chimpanzees possess certain traditions, such as ant dipping, whereas a second population possesses a different tradition, such as termite fishing. These traditions are actually rather similar, differing in the type of prey item and therefore may be local stylistic differences rather than traditions *per se*. Byrne (2007) suggests that the focus should be on technically complex behaviour patterns, such as nettle stripping in gorillas, which may be learned by cultural transmission through a community, rather than these subtle behavioural differences which may be the result of environmental differences rather than differences in transmission. In their paper, Whiten & van Schaik (2007) differ in their approach to the question of culture in animals. They suggest that although there is a lot of evidence for social learning in animals, and even some rare cases of traditions which are sustained over generations, culture is very rare. They present evidence that different chimpanzee and orang-utan populations display different cultures, and argue that while social intelligence may lead to culture ('you need to be smart to sustain culture') it is also the case that 'culture makes you smart'.

The SIH has had a dramatic influence on other areas of the biological and social sciences aside from animal behaviour. The development of the SIH was instrumental in forming the concept of mental attribution (theory of mind), which has revealed much about human cognitive development and various psychopathological disorders of social cognition, such as autism (Moll & Tomasello 2007; Reddy 2007).

Most recently, cognitive neuroscientists have used the principles of social intelligence to investigate how the brain processes information about animate agents, including work on mirror neurons and the neural basis of imitation as discussed in the paper by Gallese (2007). Dunbar & Shultz (2007) extend their earlier work which proposed that the primate brain (especially the neocortex) coevolved with processing social information, recognizing individuals and their relationships, the so-called social brain hypothesis (Dunbar 1998). Using new statistical and comparative analysis techniques, they tested the relationship between brain size and group size in the context of ecology and life history. Their analysis shows that there is a clear relationship between neocortex size and sociality, but the oft rejected idea that diet does not influence brain size in primates is seen to be ill-founded. A large neocortex can only be supported by a large brain, which is costly to run in terms of energy. A diet rich in carbohydrates and protein can supply these energy requirements, and a life-history variable, such as long developmental period, allows the brain time to grow and provides increased opportunities for learning (social and non-social). Although the relationship between brains, sociality, diet and life history is clear at the level of complex statistical analyses, Barrett *et al.* (2007), 'at the coalface' in their long-term observations of monkey's behaviour in the wild, have reviewed the primate literature and found little convincing evidence that monkey sociality is cognitively complex.

Gallese (2007) reviews his studies of mirror neurons in monkeys and humans. Mirror neurons are a class of neurons (networks) in the premotor cortex which

respond to the sight of particular actions and their associated motor patterns performed by the same individual who witnessed the actions. These neurons have been ascribed a multitude of functions, from imitation to empathy to language. Gallese (2007) expands his theory that mirror neurons are essential nodes of a 'theory of mind' network by suggesting that they play a role in linking mental states in the self with the same mental states in another (simulation). He goes further to suggest that mirror neurons allow the sharing of communicative intentions, and foster cooperation and collaboration with others (see also Moll & Tomasello 2007) through a process of empathy and embodied simulation. The notion of embodied and distributed cognition, in which we explicitly interact with our environment rather than just being passive viewers in it, is essential for how we process information (social and physical). These themes are also discussed in detail by Barrett et al. (2007).

By contrast, Frith (2007) discusses empirical studies investigating the neural correlates of social cognition, in particular 'theory of mind'. Although the field of social neuroscience is relatively new, it has struck a chord among neuroscientists. Frith (2007) reviews this work by focusing on three brain areas which have long been seen as integral components of the primate social brain network: the amygdala, the posterior superior temporal sulcus (STS) and the medial prefrontal cortex (PFC). Each of these regions plays a specific role in processing socially relevant information (amygdala—emotional valence; STS—perceiving biological motion and actions; medial PFC—thinking about mental states).

Empirical studies of how primates represent social agents are currently being used to develop robots with an artificial social intelligence, as discussed in the paper by Dautenhahn (2007). If such robots are to be integrated into society, either as tools or companions we are happy to interact with, then the design of future robots needs to accommodate thinking about how humans interact as a model (robot etiquette). This is particularly important when applying social robots in the treatment of children with autism.

Perhaps the most striking application of the SIH has been as a tool to describe how human intelligence may have evolved, how early human societies were structured and how the development of these societies leads to technological advances including farming, computers and communication between individuals living thousands of miles apart. Mithen (2007), an archaeologist, suggests a novel thesis derived from a quote by Humphrey that farming was derived from a 'mis-application' of the SIH. Mithen (2007) proposes that early humans demonstrated an enhanced cognitive fluidity which evolved from the flexibility required to process information about other social beings and their relationships. This cognitive fluidity was then co-opted for other tasks. He suggests that plants, such as squash, maize and beans in Mexico, were domesticated as an act of social prestige, to impress peers and to use in exchange for other commodities. As such, modern human cognition became more embodied due to artefacts located outside the body which represent and store information, such as books, computers and

paintings, but also domesticated crops which provided an indication of social standing. Perhaps human-like sociable robots will be seen as the greatest example of embodied cognition.

Finally, the SIH provided philosophers with material to theorize about the evolution of the human mind. In some respects, Sterelny (2007) agrees with Mithen (2007) and Humphrey that the unique aspects of our *Homo sapiens* minds did not evolve to deal with problems in the physical world. Indeed, Sterelny (2007) argues that models of human cognitive evolution which rely on keeping track of changes in the external environment alone cannot explain these unique aspects, stressing that many animals face these same challenges. Sterelny (2007) states that both the 'ecological intelligence' hypothesis and the SIH are examples of niche construction, in which the 'world' is manipulated in some way. The way that early humans foraged had a profound effect on human sociality, but also led to the evolution of technology and our subsequent unique intellectual capabilities.

In ending this special issue, Humphrey (2007) updates his earlier suggestion that the dividing line between humans and other social animals is that humans are the only creatures that have a conscious self (Humphrey 1983, 1986). He suggests that humans are alone in their capacity to think about the contents of another individual's mind. Yet, surely given the existence of Darwinian evolution, consciousness and mind-reading cannot have arrived de novo in humans. Consequently, consciousness must have some precursors in non-human animals (even if these are only at the level of sophisticated behaviour-reading) and consciousness must have been adaptive (i.e. conferred some reproductive advantage). Humphrey (2007) goes one step further by suggesting that although humans are inherently social, they are also incredibly lonely, and it is this loneliness which allows us to step back and *really* appreciate one another as individual social beings.

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Nathan J. Emery^{1,*}

Nicola S. Clayton²

Chris D. Frith³

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¹Sub-department of Animal Behaviour,
University of Cambridge, Madingley CB3 8AA, UK
(nje23@cam.ac.uk)

²Department of Experimental Psychology,
University of Cambridge, Cambridge CB2 3EB, UK

³Wellcome Department of Imaging Neuroscience,
Institute of Neurology, University College London,
London WC1N 3BG, UK

REFERENCES

- Barrett, L., Henzi, P. & Rendall, D. 2007 Social brains, simple minds: does social complexity really require cognitive complexity? *Phil. Trans. R. Soc. B* **362**, 561–575. (doi:10.1098/rstb.2006.1995)
- Byrne, R. W. 2007 Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Phil. Trans. R. Soc. B* **362**, 577–585. (doi:10.1098/rstb.2006.1996)
- Chance, M. R. A. & Mead, A. P. 1953 Social behaviour and primate evolution. *Symp. Soc. Exp. Biol.* **7**, 395–439.
- Clayton, N. S., Dally, J. M. & Emery, N. J. 2007 Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Phil. Trans. R. Soc. B* **362**, 507–522. (doi:10.1098/rstb.2006.1992)
- Connor, R. C. 2007 Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Phil. Trans. R. Soc. B* **362**, 587–602. (doi:10.1098/rstb.2006.1997)
- Dautenhahn, K. 2007 Socially intelligent robots: dimensions of human–robot interaction. *Phil. Trans. R. Soc. B* **362**, 679–704. (doi:10.1098/rstb.2006.2004)
- de Waal, F. B. M. 1982 *Chimpanzee politics*. Baltimore, MD: John Hopkins University Press.
- Dunbar, R. I. M. 1998 The social brain hypothesis. *Evol. Anthropol.* **6**, 178–190.
- Dunbar, R. I. M. & Shultz, S. 2007 Understanding primate brain evolution. *Phil. Trans. R. Soc. B* **362**, 649–658. (doi:10.1098/rstb.2006.2001)
- Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007 Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B* **362**, 489–505. (doi:10.1098/rstb.2006.1991)
- Frith, C. D. 2007 The social brain? *Phil. Trans. R. Soc. B* **362**, 671–678. (doi:10.1098/rstb.2006.2003)
- Gallese, V. 2007 Before and below ‘theory of mind’: embodied simulation and the neural correlates of social cognition. *Phil. Trans. R. Soc. B* **362**, 659–669. (doi:10.1098/rstb.2006.2002)
- Holekamp, K. E., Sakai, S. T. & Lundrigan, B. L. 2007 Social intelligence in the spotted hyena (*Crocuta crocuta*). *Phil. Trans. R. Soc. B* **362**, 523–538. (doi:10.1098/rstb.2006.1993)
- Humphrey, N. K. 1976 The social function of intellect. In *Growing points in ethology* (eds P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge, UK: Cambridge University Press.
- Humphrey, N. K. 1983 *Consciousness regained: chapters in the development of mind*. Oxford, UK: Oxford University Press.
- Humphrey, N. K. 1986 *The inner eye*. London, UK: Faber & Faber.
- Humphrey, N. K. 2007 The society of selves. *Phil. Trans. R. Soc. B* **362**, 745–754. (doi:10.1098/rstb.2006.2007)
- Jolly, A. 1966 Lemur social behavior and primate intelligence. *Science* **153**, 501–506. (doi:10.1126/science.153.3735.501)
- Mithen, S. 2007 Did farming arise from a misapplication of social intelligence? *Phil. Trans. R. Soc. B* **362**, 705–718. (doi:10.1098/rstb.2006.2005)
- Moll, H. & Tomasello, M. 2007 Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Phil. Trans. R. Soc. B* **362**, 639–648. (doi:10.1098/rstb.2006.2000)
- Penn, D. C. & Povinelli, D. J. 2007 On the lack of evidence that non-human animals possess anything remotely resembling a ‘theory of mind’. *Phil. Trans. R. Soc. B* **362**, 731–744. (doi:10.1098/rstb.2006.2023)
- Reddy, V. 2007 Getting back to the rough ground: deception and ‘social living’. *Phil. Trans. R. Soc. B* **362**, 621–637. (doi:10.1098/rstb.2006.1999)
- Silk, J. B. 2007 The adaptive value of sociality in mammalian groups. *Phil. Trans. R. Soc. B* **362**, 539–559. (doi:10.1098/rstb.2006.1994)
- Sterelny, K. 2007 Social intelligence, human intelligence and niche construction. *Phil. Trans. R. Soc. B* **362**, 719–730. (doi:10.1098/rstb.2006.2006)
- Whiten, A. & van Schaik, C. P. 2007 The evolution of animal ‘cultures’ and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)