trans-Atlantic migration lasting a period of years. Turtles enter the North Atlantic gyre, a circular current system that flows around the Sargasso Sea, and many cross to the eastern side of the Atlantic before returning to North America. The turtles have a strong need to remain within the gyre: if they stray too far north they risk death in cold waters, whereas going too far south may cause them to be entrained in south Atlantic current systems and carried far away.

Young loggerheads apparently use the Earth's magnetic field as a source of positional information to help them remain within the gyre system. The Earth's field varies across the surface of the globe in such a way that each oceanic region has a unique magnetic field. When a young turtle encounters a magnetic field that exists near the northern boundary of the North Atlantic gyre, it responds by swimming south, whereas a field from the southern boundary of the gyre elicits swimming toward the northwest (a response that presumably leads a turtle back toward North America). These responses to magnetic positional information appear to be largely inherited, given that they are present in turtles that have never been in the ocean.

Is the magnetic field of the Earth used by coastal juveniles and adults as well? Juveniles living in coastal feeding grounds use the Earth's magnetic field in an even more sophisticated way. Rather than responding to magnetic fields that mark boundaries, older turtles apparently learn the magnetic topography of the geographic areas in which they feed. The turtles can then use magnetic cues to help them navigate back to particular areas.

The existence of a 'magnetic map' in sea turtles was demonstrated by exposing juvenile green turtles (*Chelonia mydas*) to magnetic fields that exist in locations north or south of their feeding area. Even though the turtles were tethered in a pool of water close to their feeding grounds, those exposed to a

magnetic field that exists several hundred kilometers to the north swam south, whereas those exposed to a field from the south swam north. Thus, the turtles can use positional information in the Earth's field as a kind of map that helps them navigate toward specific locations.

Whether adults use magnetic information in natal beach homing is still unknown. A plausible scenario is that the turtles imprint on the magnetic signatures of their natal region, allowing them to navigate back when it is time to reproduce. This strategy, if it is used, might also work in combination with detection of other environmental features like visual landmarks or chemical cues.

How do sea turtles detect the Earth's magnetic field? No one knows for certain how any animal detects the Earth's magnetic field. One idea is that crystals of the magnetic mineral magnetite are coupled to the nervous system and function as receptors for the magnetic sense. Magnetite particles have been detected in sea turtles, migratory birds, and some other magnetically sensitive animals. A different hypothesis, however, is that magnetic field detection might be accomplished through a complex series of chemical reactions that are associated with the visual system. How sea turtles detect magnetism remains a mystery.

Where can I find out more?
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Social cognition

Klaus Zuberbühler and Richard W. Byrne

The question of why humans possess superior cognitive skills has a long history in science. One important idea is that human intelligence has evolved in the social realm [1]. The rationale is that individuals who cooperate and compete well in a social setting do better and produce more offspring than less skilled individuals, and that these skills are heritable. The conditions for the evolution of social abilities may have been especially favourable in primates. Most primates live in individualised societies that are characterised by kin-based social networks, a situation that may have triggered an evolutionary arms race in social skills.

Social cognition concerns an individual's ability to interact socially in an intelligent way. As it is near impossible to define intelligence objectively, a common research strategy has been to select a well-described human skill and investigate the degree to which it is present in animal subjects. Episodic memory is a good example. A series of studies with food-caching birds has revealed that these animals are perfectly capable of mentally 'traveling backwards in time' to recollect specific events in the past [2]. Oddly, less evidence for episodic memory has been found in non-human primates, although a study by our group [3], published recently in *Current Biology*, has shown that monkeys take past weather conditions into account when searching for food.

One empirical approach to social intelligence is to investigate animals' ability to recognise others' social relations and to predict their behaviour. Research on the formation of social concepts has been particularly important and has revealed some intriguing similarities between human and animal mental abilities. One study [4], with long-tailed macaques, has

become something of a classic. Monkeys were trained to select photographs of familiar group members, either mother–offspring dyads or other pairings. The study animals then successfully mastered novel combinations, demonstrating that they possess a social concept analogous to the human mother–child affiliation. We now know that primates can build up social knowledge from observations alone. After watching video clips of agonistic interactions between two unfamiliar conspecifics, rhesus monkeys were able to select the dominant individual in each interaction, and individuals were able to transfer their skill to novel video clips [5].

Under field conditions, such complicated techniques cannot be applied, and experimental work typically relies on much simpler paradigms. A successful approach has been to monitor vocal behaviour during social interactions, and to use the observed patterns as a basis for field playback experiments. Subordinate female baboons, for example, tend to produce fear-barks to a more dominant individual approaching them. Dominant females respond with grunts, especially if they desire to interact peacefully. These types of exchanges have successfully been used to mimic different types of social interactions for nearby listeners. In one particularly elegant experiment [6], baboons not only recognised the rank orders of the different group members, but they also understood to which matrilineal kin group the individuals belonged, demonstrating that primates organise social concepts in a hierarchical way. These and other studies indicate that Sapir's [7] famous proposition that a "concept does not attain to individual and independent life until it has found a distinctive linguistic embodiment" is just not supported by the empirical evidence.

The biological function of social cognition
Dealing with conspecifics and other competitors
Another way of recognising social intelligence is by investigating an individual's ability to create

Figure 1. Living in large individualised groups with complex kin-based social networks favours individuals who are skilled at solving social problems. (Photo © Klaus Zuber-bühler.)

insightful and novel solutions that are not just the result of a blind trial-and-error approach [8]. Fast learning, powerful memory capacities, and the ability to shift representations on a mental 'game board' are all prerequisites for innovation. The animal literature is full of examples of seemingly insightful behaviour, although often in response to physical problems. In the social domain, progress has been made with observations of tactical deception in primates, cases where conspecifics are manipulated into acting on false information [9]. Tactics are probably mostly learned from experience, and not necessarily understood as deliberate changes of mental state. The extent of innovation is usually limited to using a familiar action in a novel context. The use of deception is by no means randomly spread across species, however: it covaries with the size

of the neocortex, and neocortex volume has also been found to correlate with group size in primates [10].

These facts support the 'Machiavellian intelligence' or 'social brain' hypothesis, which proposes that large brains are an adaptation to the social complexity produced by living in long-term social groups. Social tactics that seem sophisticated, such as deception and cooperation, may be built on quite simple cognitive mechanisms: the main thing that is needed is efficient memory, to differentiate individuals and keep track of the webs of kinship, dominance and mutual favour-trading that make up simian social life (Figure 1). Presumably, similar levels of social complexity could be created in inter-specific associations, such as coral reef fish communities, and these could be used to test the association with brain enlargement [11].

Dealing with predation by social means

Predation is one of the most powerful forces of natural selection, but it is not normally linked with cognitive evolution. A common adaptation to predation is the formation of social groups, in which individuals benefit from dilution effects and other simple 'safety-in-numbers' benefits [12]. However, non-human primates may not benefit much from these advantages, because group members are often highly related to each other: losing a group member typically means losing a close relative. As a consequence, losing a genetic relative is a highly traumatic event for a primate [13]. The kin-based group structure, moreover, spoils some of the benefits of simple safety-in-number advantages that other groups of animals can profit from. It is interesting in this context that most forest primates have a strong tendency to form poly-specific associations, sometimes containing over half a dozen different monkey species, presumably to exploit mutual safety-in-number effects by associating with individuals to whom they are not related.

At the same time, primate kin-based groups appear to have served as a platform for the evolution of cooperative behaviours that require more advanced cognitive abilities. One particularly striking act of altruism is alarm calling. In Diana monkeys (Figure 2), alarm calls serve to name predator classes and thus inform nearby hearers about the nature of the danger, irrespective of urgency or other threat-related variables [14]. Diana monkeys have also been observed to eavesdrop on the vocal behaviour of other species, in some cases even the predators themselves. Campbell's and putty-nosed monkeys are able to alter the meaning of their alarm calls by constructing more complex call combinations, and most forest monkeys use alarm calls to communicate directly to predators to disable stealth hunters [14,15].

In these contexts, individuals often behave as if they use simple deductive processes to
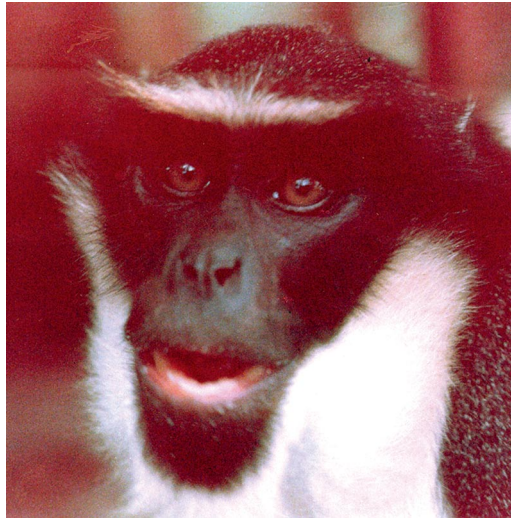

Figure 2. Diana monkeys exhibit sophisticated cognitive abilities when interacting with conspecifics and other species. (Photo © Klaus Zuberbühler.)

make optimal use of the available acoustic information. For instance, when hearing the alarm calls of crested guinea fowl, a gregarious terrestrial forest bird, Diana monkeys typically respond as if they had seen the birds' major predator, a leopard. When the context was experimentally altered, such that it appeared that the birds' alarm calls were given in response to a human poacher rather than a leopard, the monkeys remained silent, the most adaptive response to human poachers. These and other studies suggest that primates respond to the most likely cause of calls, rather than the calls themselves [14].

In sum, during predation events, primates regularly exhibit behavioural patterns that are typically regarded as indicators of advanced social intelligence, being based on understanding the predator and prey hierarchy, other species' communication systems and the underlying reasons for signal production. Predation may have created complex problems similar to those encountered in social situations — or perhaps even greater. Not only is cooperation and competition with conspecifics involved in both cases, but to avoid predation individuals also need to interact with and predict the behaviour of other prey animals and the predators themselves. Selection pressures are high because behavioural errors can lead to the loss of life, while this is rarely the case during other social

interactions. Primates have no weapons or safe microhabitats to protect themselves against predators, and their cognitive abilities appear to be their most powerful tools [16].

Enlarging the diet set by social means

The problems created by within-group complexity and predator avoidance apply to both monkeys and apes, in proportion to (respectively) their group size and predation vulnerability. However, many researchers have noted that one taxon, the great apes, appears cognitively advanced compared to monkeys, even though the apes live in no larger groups and their size renders them less vulnerable to predation than most monkeys [17]. This puzzle has led theorists to examine possible environmental challenges that might have selected for more advanced cognition, highlighting the fact that all great apes — and few if any monkeys — deal with mechanically tricky feeding or locomotor tasks in their daily life [18].

Even here, social cognition may come into play. Where complex skills are needed to obtain and process hidden or physically defended food items, social companions present a potential source of valuable knowledge: the extent to which an individual can tap this knowledge depends on its abilities in social learning. Simple forms of social learning are available to many species,

but to learn elaborate skills by observation requires the ability to 'parse' another behaviour, thereby understanding how to replicate the effective actions [19]. From understanding another's behaviour it is a small step to understanding their plans and reasons for carrying them out, and a case can be made that human capacities to understand mental states derive ultimately from selection pressures on non-human apes to learn complex feeding skills (Figure 3).

The limits of animal social cognition

Despite these examples of apparently intelligent behaviour, non-human primates and other animals are also remarkably limited in some of their cognitive capacities. A cardinal aspect of human cognition is the ability to take the mental perspective of another individual, sometimes called 'theory of mind' or 'mentalizing' ability. In its fullest sense, this ability is restricted to humans, but some animals show certain component abilities. For example, scrub jays are able to predict the movements of a competitor, based on assessing its visual perspective and recent history of interaction, an ability also found in chimpanzees [20,21]. Related to this, when interacting with a human experimenter who is looking behind a barrier, some corvids and great apes position themselves such that they can see what the experimenter is looking at, suggesting that they attempt to take the experimenter's visual perspective [22,23]. Yet, chimpanzees, and perhaps non-human animals in general, have difficulties sharing attention and intention with others.

A variety of evidence suggests that these psychological processes are pivotal for language acquisition and other culturally transmitted behaviours in humans. Although primates have intentions and can recognise those of other individuals, they apparently lack the ability or motivation to share them [24]. A good diagnostic for shared intentionality is an individual's attempting to re-engage a

Figure 3. A new-born mountain gorilla has ample opportunities to watch skilful and complex foraging activity before it meets the challenge of extracting food from hidden or defended sources. (Photo © Richard Byrne.)

partner who suddenly stops a cooperative interaction. Children reliably start to communicate to reluctant partners, something that is not observed in chimpanzees. Hence, although non-human primates can engage in simple cooperative acts, and appear to have some understanding of others' intentions, they seem unable to converge on and uphold a state of shared intentionality [25].

Conclusions

Most theoretical advances concerning the evolution of social cognition have emerged from research with human children and non-human primates. The two groups are remarkably similar in many aspects of social cognition, but some striking differences have been observed. Only human children are able to go beyond perspective taking and engage in true mentalizing. Related to this, only children are able to jointly attend with a partner to an external object and to engage in coordinated, cooperative interactions that are based on understanding and sharing of intentions, perhaps the cognitive

basis for ratcheted cultural developments of humans.

Although the social domain appears to be a particularly rich breeding ground for the evolution of intelligence, it is noteworthy that a large number of primate species, including most apes, live in comparatively small groups with relatively simple social networks. Baboon-like large and socially complex groups, composed of many reproductively active males and females, which generate a continuous stream of social challenges, are not necessarily typical for primates. It is also not clear whether it is right to assume that social complexity increases with group size, especially if individuals are interested in the social relations of only a select number of particular group members.

We have mentioned two additional potentially important contexts, in which advanced social abilities are likely to evolve due to the significant fitness benefits provided for the individual: the ability to avoid predators and the ability to enlarge diet by social means. In both contexts, success is based on behaviour reading

and appreciation of the underlying mental processes. It is also the case that some of the most relevant problems encountered by primates possess both a social and an ecological dimension, which are often intrinsically entangled. For example, avoiding predation depends on an individual's ability to predict a predator's behaviour as well as on its social skills in gaining the anti-predator benefits generated by group-life, and learning complex skills depends on tapping the accumulated skill base of other group members. Empirically sorting out the relative contribution of these different evolutionary forces is no trivial undertaking.

Finally, the vast majority of empirical research on social cognition has been conducted with primates, probably because researchers interested in these questions prefer to work with phylogenetically close relatives. However, there is no reason to assume that the same principles and evolutionary pressures have not acted on other groups of animals, and that some non-primate species possess comparable social intelligence. The current literature is consistent with the idea that natural selection does not need a primate brain to endow it with social intelligence. An important challenge for the future, thus, will be to determine in what ways other groups of animals, such as corvids or social carnivores, are similar to or differ from primates in their social intelligence or in the underlying motivation to display it.

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Does reduced heterozygosity depress sperm quality in wild rabbits (*Oryctolagus cuniculus*)?

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Gage *et al.* [1] recently reported an association between microsatellite heterozygosity and male reproductive traits in a sample of rabbits (*Oryctolagus cuniculus*) collected from across the UK. Based on this finding, the authors claimed their results to be a rare demonstration of inbreeding depression for sperm quality in the wild. Here, we challenge this interpretation and suggest that the evidence for inbreeding depression is weak. The basis for our criticism is that the analysis of Gage *et al.* [1] does not adequately deal with population stratification.

Gage *et al.* [1] studied rabbits from twelve geographically isolated populations, for which the sample sizes in the key analyses were 29, 13, 13, 9, 9, 6, 4, 2, 2, 2, 1 and 1. The authors have previously demonstrated strong population differentiation between UK rabbit populations [2]. It is well known that sampling from different geographic or ethnic sources can lead to spurious associations between marker genotypes and phenotypes [3].

The authors performed two analyses to address the possibility of confounding between genetic and environmental determinants of male reproductive traits. First, they treated all rabbits as independent data points. Second, they looked at the regression of population mean sperm quality on