

# Sociality, Evolution and Cognition

# Review

Richard W. Byrne and Lucy A. Bates

Variations in brain size and proportions can be linked to the cognitive capacities of different animal species, and correlations with ecology may give clues to the evolutionary origins of these specializations. Much recent evidence has implicated the social domain as a major challenge driving increases in problem-solving abilities of mammals. However, the methods of measurement available to researchers are often indirect and sometimes appear to give conflicting answers, and other intellectual challenges may also have been influential in cognitive evolution. While the cause of an evolutionary increase in intelligence may be domain-specific (sociality, for example), and the brain specialization that results may largely implicate a single perceptual system, such as vision, the intelligence shown in consequence can be very ‘general-purpose’ (as in primates and some avian taxa). Future research needs to get beyond vague ascription of ‘greater intelligence’ or ‘faster learning’ towards a precise account of the cognitive mechanisms that underlie particular mental skills in different species; that will allow theory-testing against data from complex, natural situations as well as from the laboratory, on a common metric.

## Introduction

Animals vary dramatically in brain size, both in absolute terms and as a fraction of overall body size. Why should this be? Brain tissue is metabolically expensive [1], so evolutionary investment in brainpower comes at a price, and we therefore expect large-brained species to be ones whose survival depends on dealing with serious cognitive challenges [2]. The particular nature of those challenges may give clues to the evolutionary origin of intelligence in that lineage. Special attention has historically been given to the origin of primate intelligence, with the aim of throwing light on the evolution of human cognition. In order to test among competing theories, the method generally used has been to correlate brain size with various estimates of cognitive challenge, across a range of species. This approach has led to the accumulation of considerable evidence for a slightly surprising idea: that social living, even more than the obvious environmental challenges of finding enough to eat and avoiding being eaten, has been responsible for specialization in intelligence [3–7]. In non-human primates, insectivores, carnivores, ungulates, insectivorous bats and cetaceans, a common pattern has been found in the relationship between brain size and typical group size of the species: the larger the group, the larger the brain [8–11].

By contrast, measures of environmental complexity, such as range area, day journey length, diet type and how food is obtained have usually turned out to be unrelated to brain size. It seems that dealing with social problems may, for a wide range of mammals, be the biggest intellectual problem to be faced: and perhaps the extraordinary human brain has humble origins in the social problems of our remote primate ancestors [12].

There are, of course, quite a lot of assumptions in this simple account. The variables — intelligence, cognitive challenges of social life and ecology — cannot be measured directly, so measurable things (such as brain size, group size, range area, and so on) have had to be used as proxy variables: do these really represent what they are supposed to represent? Sociality is treated as varying along the simple scale of total group size, but there are many reasons why an animal might be social: do these all have equivalent effects? Certainly it makes sense that a larger brain reflects a greater need, but what is ‘large’: large in absolute number of neurons or large in comparison to the animal’s overall body dimensions [2]? The brain has an immense range of functions, and function does not necessarily map neatly onto neural structure: can the particular areas, whose enlargement appears to result from selective pressures to solve social problems, be distinguished from overall scaled increases [13]? Usually, the tightest correlations have been found between social group size and the neocortex, an area that is conspicuously enlarged in several groups of large-brained mammals, including primates, carnivores and cetaceans. Does it thus make sense to treat the neocortex as the ‘thinking part’ of the mammalian brain? Not all of these issues can be decided on present evidence, but we return to several of them later in this review. We begin, however, by explaining the ‘social intelligence’ theory in more detail, in order to examine the extent of its success in understanding the evolution of advanced cognition. Then, because other cognitive challenges may also have caused increases in brain capacity, we ask: is social intelligence separable from general intelligence, and what cognitive mechanisms constitute the rather vague idea of ‘intelligence’ in non-human animals?

## Machiavellian Intelligence

Group living has many possible advantages for animals, most obviously in minimizing predation (by increased vigilance or dilution of risk) or allowing cooperation (in locating food or hunting prey). But living in close proximity to conspecifics also has clear disadvantages, in terms of direct resource competition. The tension between aggregation and dispersal is vividly illustrated in the daily fission–fusion behaviour of baboons (*Papio papio*) living in arid Sahel habitats that they share with a range of predators [14]. At night, aggregations of hundreds of baboons sleep together, but when foraging, these groups split up into tiny parties of three to eight individuals, efficiently

re-aggregating in the heat of the day at shady drinking places by homing in on loud calls from other sub-groups [15]. This separation and re-joining of groups allows each individual to benefit from the dilution effects of 'being one in a crowd' when most vulnerable to predation [16], while reducing competition at food patches.

Permanent group living is thus a demanding evolutionary option, as resource competition tends to disrupt group stability: in mammals, however, there are several taxa — such as primates, cetaceans and carnivores — in which long-lasting social groups are regular and conspicuous. The key is that an individual that can use its intelligence to acquire resources by stealth or cooperative tactics may be able to retain the benefits of group living on a more permanent basis. Niccolo Machiavelli famously recommended politicians to use social manipulation for individual profit, hence the term 'Machiavellian intelligence' for the idea that social manipulation has been favoured in animal evolution [17]. (Note that, as Machiavelli himself pointed out [18], the most effective manipulator is often the most trustworthy, cooperative and respected member of society: the synonym 'social intelligence' emphasises these pro-social traits, but ultimately the genetical benefit is a selfish one.) Critically, it is argued, other individuals present a 'moving target' of continually changing behaviour, able to respond to the self's strategies with their own [5]: social complexity presents an inherently greater intellectual challenge than environmental complexity.

The logic of this theory will only apply if a social group is a semi-permanent aggregation: not all sociality is cognitively demanding. Temporary groupings, such as flocks of non-breeding ducks on lakes, migrating herds of ungulates, or fish schools attacking krill are not predicted to have any such selective effect on intelligence. Similarly, multi-species groups, such as the huge assemblies regularly found in tropical bird species, can provide predator protection by vigilance and dilution, whilst minimizing the costs of competition since different species will tend to occupy somewhat different feeding niches [19]. Aggregations which are both temporary and multi-species have even been noted: for instance, baboons and impala associate together, and here the different perceptual strengths of a primate and an ungulate may give additional advantage in avoiding stealth predation. As with Neotropical bird flocks, diet difference helps minimize competition, reducing the cost of association compared to the case of long-lasting groups of conspecifics.

Enticingly, most reports of apparently 'smart' behaviour in mammals come from the relatively few species that are semi-permanently social, consistent with the social intelligence proposal. Unfortunately, comparative psychology has found no acceptable 'intelligence' test for animals' [20], so researchers have turned to measures of brain size to further examine the effects of sociality. Positive correlations have been found between mean social group size and neocortex volume (whether measured in absolute terms, or in proportion to the size of the rest of the brain) in all mammalian groups that have so far been examined

systematically [8–11]. Moreover, in catarrhine primates (Old World monkeys and apes), group size also correlates with the amount of time individuals spend in social grooming [8,21], suggesting that these primates need to spend more time building up networks of potential allies if they live in larger groups. And just occasionally, there has been an opportunity for direct assessment of animals' use of social manipulation, for instance in the case of primate tactical deception, where data were amassed from many studies over a wide range of species [22] (Figure 1). Of course, observer-effort tends not to be uniform across species, and frequencies of deception needed to be corrected for effort. Then, deception was found to be well predicted by neocortex volume but not affected by rest-of-brain volume [23].

These three facts have led to widespread acceptance of the theory that a major evolutionary stimulus to brain enlargement in social mammals has been the need for a larger neocortical area to facilitate more effective social manipulation, including the need to keep track of a complex network of social relationships [24–26].

### Measuring Brainpower

The high costs of investment in brain tissue mean that, when a brain is large in relation to lean body mass, it is a sign of strong selection for problem solving of some kind [27]. Over longer evolutionary time-scales, however, this effect may disappear: relatively large brains are a serious liability, inevitably resulting in evolutionary pressure for increased body size. Whether such change will indeed happen depends on other environmental circumstances, of course; the metabolic demands of flight, for instance, will make increasing body size disproportionately costly for birds and bats, and more generally metabolic rate will constrain brain size [28].

Brain size relative to body size is not a good measure of cognitive power, because like any computational system the brain's power is ultimately dependent on absolute number of components. Artificial computing systems are also limited by computing speed, but this may be less important in vertebrate brains. True, nerve conduction speed varies with the diameter of myelinated fibres, and fibres are relatively thin in the toothed whales and elephants, whose brains contain as many cortical neurons as those of humans despite the higher cell packing density of human neurons [29]. Thus these very large mammals may have been somewhat liberated from any evolutionary pressure for neural efficiency; but in general it is perhaps safest to assume brain parameters are computationally optimal for a given brain's size and organization.

Thus, some measure of absolute size is more likely to index animal intelligence [27,30]. In comparative studies of the mammalian neocortex, several different measures have produced mutually consistent results: absolute volumes, with rest-of-brain volume as a control variable; ratios in linear proportion to rest-of-brain; residuals of scaling function between neocortex and rest-of-brain [8,31].



Figure 1. Deception allows female gorillas a choice of mating partner.

(A) A female gorilla solicits a young silverback with head-flagging movements to remain behind with her when the group moves on. They subsequently mated surreptitiously, suppressing the normal loud copulation calls; the older, leading silverback of the group would not tolerate such mating if detected. (B) Here, the leading silverback catches the 'secret mating' partners in the act; note that the eyes of both partners are focussed to the left of the photographer, on the male who proceeded to punish the female with violence.

### Comparing Theories: Estimating Cognitive Challenge

To find which source of environmental complexity best predicts variations in species' brain size, it is necessary to make some rough-and-ready estimates of the problems animals face. As we have seen, the usual approach is to treat the mean size of semi-permanent groups as an indication of the social challenge. The logic is that, if the problems arise from 'other people', then the severity of problems must increase at least linearly with the number of others that one lives with. (In fact, animals may never socialize with every other group member, restricting their efforts at building up alliances to a smaller clique. But clique size has been shown to increase with mean group size, so the approximation is fair [32].) However, if a particular species has a more refined cognitive understanding, then individuals of that species may have a lot more to notice and remember about others than members of a less discerning one: so there is an element of circularity. Monkeys, at least, recognize other group members as individuals, by their voices and their appearance [33]; they know who is close kin to whom, and who outranks whom [34,35]; they recall and repay favours by their allies [36–38]; they invest grooming time building up a network of reliable allies, and

make an effort to reconcile with those allies if they should come into conflict [39,40]; and they notice whether interactions among third parties follow the 'usual' rules of who is dominant or submissive to whom [41]. For these species, then, memory load for social information becomes very significant as group size rises (Figure 2).

For primates, the major alternative theory that has been tested against Machiavellian intelligence is that of ecological cognition. Primates generally must build up an adequate nutrition from dispersed, largely vegetable foods in complex tropical environments. It has been argued that remembering where the key resources are and when they fruit poses a significant intellectual challenge [42,43]. In addition, some foods are hidden, embedded in substrate or inedible casing, and specialization on embedded foods has also been suggested to require more imagination than eating foods open to direct perception [44,45]. However, when proxy variables have been devised to estimate the extent of the environmental memory problem — day journey length, home range area, proportion of embedded foods — they have not been found to correlate with species brain size [46,47].

Admittedly, frugivorous primates have systematically larger home ranges, and larger brains for their

Figure 2. Elephants also have large brains and complex societies.

Although the small number of species in the *Proboscidea* has prevented comparative analyses of the kind that in other taxa have linked group size to brain enlargement, elephants do possess very large brains and remarkably complex societies.



body size than folivorous ones [48]. But this effect may reflect selection for larger bodies in folivorous species, rather than larger brains in frugivorous ones [27]. Specializing on coarse, leafy material requires a large or compound gut, inevitably tending to make the body large. Species pairs that differ in this way, like the gorilla and the more frugivorous chimpanzee, have closely similar brains but very different body weights. As noted above, using brain size relative to body size is a good way of estimating the strength of evolutionary selection pressure (and thus the *need* for a large brain), but no way to judge the *cognitive potential* of the brain. There is little current evidence that memory for food — the cognitive map hypothesis — has contributed greatly to the evolution of large brains among mammals.

Another ecological theory has yet to be fully evaluated. This is that a key cognitive challenge was to ensure successful hunting (by predators) and avoidance of predation (by prey) [49]. As with Machiavellian intelligence, predator-prey interactions have the property of a 'moving target': the individuals that present the problem are continually acting and reacting in order to thwart the other. And since the result may involve death the likely selection pressure on mental mechanisms that give any cognitive 'edge' is very great. There are a number of suggestive facts in favour of this theory. Jerison showed that the relative brain size of successive radiations of Holarctic carnivores and ungulates increased steadily from the Paleocene to the Pliocene, apparently in tandem but with the relative brain size of carnivores always slightly ahead of that of ungulates [2]. In contrast, the Neotropical herbivores of the same period, in a continent that lacked significant mammalian predators, showed no such systematic increase in brain size over time. In a natural experiment, the cranial fossils of a Majorcan bovid showed a striking drop in brain size after its only mammalian predator died out (Figure 3) [50]. And among living species, the most complex systems

of representational communication yet discovered, in monkeys, function to enable highly specific predator warnings to be given to other group members [51]. Social living, therefore, gives these monkeys extra benefits in predation reduction, on top of any 'selfish herd' dilution effects, when the group becomes a cooperative machine for outwitting the predator.

Unfortunately, estimating predation pressure is generally nigh-on impossible in most environments: predators are, by the nature of their livelihood, hard to find and count. Moreover, teasing apart cognitive effects that result from predator-prey interaction from those that result from within-group social problem solving will be particularly tricky when the ultimate, functional reason for group living is often the minimization of predation, anyway [52]. And apart from primates, many of the social mammals that show particularly large brains are also themselves predators, for example carnivores and toothed whales [53]. (At least one social carnivore, the spotted hyena, even displays remarkably monkey-like social organization [54].) At present, it must be admitted that no broad, comparative analysis points to predation as a major source of cognitive advance in evolution; but it would probably be unwise to dismiss the idea.

In principle, the most rigorous test of the Machiavellian intelligence hypothesis would be to compare the cognitive skills of a social animal with those of a non-social, matched 'control' species — one that is closely related, ecologically similar, and so forth — and repeat this exercise for many such matched pairs. This approach is fraught with problems of finding appropriate control species, however. How closely related should these species be? How similar should the niches the species occupy be in order to claim comparable ecological challenges? And arguably the most difficult to reconcile: what tests or measures can be used fairly and reliably to compare the cognitive skills of the different animals? Tests must be ecologically valid and physically possible for all species under



Figure 3. Brain size decreases in the absence of predation risk.

The right-hand skull, with brain endocast to scale, shows *Myotragus balearicus*, a Miocene bovid species that inhabited Majorca at a time when all major predators had died out. In contrast to the small brain of *Myotragus*, Miocene bovids of the same body size retained large brains if they inhabited continental Europe, where carnivores remained a threat. The left-hand skull is that of *Rupicapra rupicapra*, sister taxon to *Myotragus*. (Picture acknowledgement: Dr Meike Köhler.)

comparison. But such species-fair tests of animal intelligence are, as we have noted, currently non-existent.

In the face of these difficulties, the most productive approach so far has been very different: the meta-analysis of written reports of behaviour [55], comparing well-defined but broad categories of behaviour, such as tactical deception, tool using and behavioural innovation. These analyses have allowed comparisons of the behavioural flexibility of many species at once, illustrating how the use of ‘smart’ behaviour varies predictably with social group size and neocortex size, at least in primates. The emphasis on primates is currently inevitable, but more reports of pertinent behaviours from other species should become available as interest in cognition spreads among zoologists. Moreover, increasing understanding of brain organization in non-mammalian taxa should allow use of the comparative method to track evolutionary pressures on the functional subsystems of their brains. This should ultimately allow a broader understanding of the origins of vertebrate cognition.

#### How Widespread Might Social Intelligence Be?

As we have noted, brain tissue is metabolically costly; also, the need for energy to be supplied to the brain is remorseless — even a short interruption causes loss of tissue — and increased head size may cause other adverse effects, such as birth difficulties in viviparous species. Large brains are perhaps best avoided, then, and if they are essential for living in semi-permanent groups we might expect vertebrate sociality to be rare. This indeed seems to be the case: in amphibians, reptiles and fish, aggregations are usually temporary or absent. Convincing reports of advanced cognition are scarce in any of these species, consistent with the presumption that they can deal with environmental problems in ways that do not rely on the flexibility for which cognitive mechanisms are needed. (The cognitive abilities of some coral-reef fishes [56–58] are a conspicuous exception to this generalization, and may prove to be a convergent case of selection for Machiavellian intelligence in a socially complex community of many sympatric species.) Even in birds, most species are socially monogamous (even if breeding is

colonial) and single-species flocks are usually seasonal or ephemeral. To the extent that there is any variance in semi-permanent group sizes of birds to examine, it is not a good predictor of brain size [59].

It would therefore be tidy to report that birds, like other non-mammalian vertebrates, lack signs of specialization in advanced cognition. This is not the case, however. Two avian taxa stand out, the parrots and the corvids, both in manifest intelligence and in brain size — relative to body size and, for the larger species, in absolute terms. Extensive experimentation with an African grey parrot, Alex, has revealed an impressive range of abilities: referential use of spoken words, understanding of number, use of relative concepts and same/different judgements, and so on [60]. The even larger brained cockatoos and macaws have yet to be examined for cognitive capacities, but the tiny spectacled parrotlet has been found to label specific individuals vocally [61].

Among corvids, remarkable abilities have been found in a range of species [62]. Clark’s nutcrackers make several thousand caches of pine seeds each autumn, and retrieve them over the winter and spring. In the laboratory, they have consistently outperformed other, non-storing birds in spatial memory tasks [63]. Scrub jays take account of the decay-rates of cached food of different types when deciding which of their caches to excavate and consume [64]; they take account of the viewing opportunities of competitors when deciding where to cache [65]; they re-cache food in new places, if competitors might have seen their original cache sites [66]; and they take account of which individual competitors have seen them make caches, when deciding which to consume first or re-cache in private [67]. Ravens use competitor’s gaze direction when hiding food, distinguish between knowledgeable and ignorant competitors, and use several tactics to deceive them about location of foods [68,69]. Rooks readily learn to retrieve food from a tube with a gravity-trap in it, whereas monkeys have proved inept at similar tasks [70]. These impressive abilities are not obviously related to the birds’ degree of sociality: rooks are colonial and feed in temporary feeding flocks, scrub jays may live in extended families, ravens are monogamous but form flocks as juveniles,

whereas grey parrots and nutcrackers are monogamous and rather solitary species. Even where birds show social manipulation, it is directed at outsiders rather than group members.

While the social problem solving needed to live in a large group may be an important stimulus to cognitive development, it is clearly not the only one. At a more general level, the repeated need to deal competitively with *minds* — minds of familiar social companions in a long-lasting social group, minds of observant and perhaps individually known competitors in a crowded foraging environment, or minds engaged in the life-and-death struggle of predation — may always select for greater cognitive ability. Wrestling with other minds guarantees that only highly flexible, responsive mechanisms confer real advantage. Thus, rather than being seen as competing, mutually exclusive hypotheses for the evolution of intelligence, the Machiavellian intelligence of social living and the cut-and-thrust of predator-prey relations may be just two facets of the same thing.

#### Is the Result a ‘Domain-Specific’ Intelligence?

If the advantage gained from efficient and skilful social manipulation does indeed lead to enlargement of all or part of the brain, is the outcome a brain specialized for social problem solving, but perhaps inept at other cognitive tasks? This question resonates with an old debate in psychology: is intelligence a single propensity to deal with all kinds of information efficiently, or are there different ‘intelligences’ for different skills? That historic debate cast the question in terms of whether a single number, the value of ‘g’, describes a person’s intelligence, or is intelligence modular, so that each module might be more or less advanced [71]. It must be admitted that psychology did not settle the matter for human psychometrics, largely because the discussion often degenerated into advocacy of rival statistical methods. However, because the differences in ability between different species may be expected to be on a larger scale than the subtle interpersonal variance within humans [72], it may be possible to make more progress.

Looking at positive evidence of cognitive sophistication in animals, many of the most striking cases certainly concern social understanding and social manipulation: several examples have been given already. The ability of monkeys, in particular, to notice and communicate about very subtle social nuances has been set in stark contrast to their seeming ineptitude in reacting to the physical world [35]. Critical in this debate were a series of experiments simulating the presence of bizarre natural history events — for example, a hippopotamus calling from a desert area — or physical cues to the presence of a dangerous predator — such as an antelope body draped over a branch, characteristic of leopard kills, or a broad straight groove in the sand, characteristic of a large python track. Vervet monkeys showed no interest in any of these set-ups, even those apparently signalling the presence of their major predators [73].

But it is famously difficult to make firm deductions from negative evidence — maybe the monkeys were

able to detect the falseness of the set-ups, or maybe making dramatic reactions to every sign of a predator would be counter-productive. More recent work, showing that monkeys use the referential calls of other species, and use memory to reason which danger is actually present when they hear ambiguous alarm calls, brings into serious question the proposal that monkeys are poor at natural history [74–76]. Rather, perhaps it is their closed repertoire, especially their apparent inability to acquire new motor patterns for their hands — compared with the great apes, whose manual repertoire seems productive and open [77,78], and who readily develop skilful tool-use — that restricts the ways in which they are able to show their understanding of the physical world.

The broad, comparative approach that showed neocortex size to be a good predictor of social manipulation might seem to point to the neocortex as a module of social intelligence. But in fact a large neocortex has been found to correlate with frequency of other signs of intelligence in primates: learning from companions, tool use, and innovation in behavioural repertoire [79]. It looks as if neocortex size, for primates at least, is best seen in terms of ‘g’ rather than a specifically social module [80]. Selection for social manipulation may be what led to the development of large brains, but the resulting problem-solving abilities have pay-off in quite other areas. Advanced cognition also appears domain-general in corvids, rather than restricted to food-getting and food-storing domains. Partnerships in rooks and jackdaws share some of the characteristics of primate alliances [59], including reciprocal aid and postconflict affiliation [81], and like monkeys, pinon jays can learn another bird’s rank from third-party observation alone [82].

The evolutionary origin of these social skills is unlikely to be the challenge of social living, as we have noted, because the tell-tale correlation of brain enlargement and social group size is missing. It must be admitted that comparative analyses of brain evolution are still in their infancy. Birds have a very different brain organization to that of mammals, with whom they most recently shared an ancestor over 250 million years ago, and identifying homologous structures in bird and mammal brains is fraught with difficulty. Researchers attempting direct comparison with mammals thus often find disorder [83]. Where orderliness has been found, however, it is measures of innovation frequency and the use of objects as tools, derived from meta-analysis of an extensive amateur literature, that show clear relation to brain enlargement in birds [84,85]. Any convergence between corvids and primates must therefore be at the level of domain-general intelligence. In the case of parrots, whose range of abilities again suggests a domain-general intelligence but which are only very distantly related to corvids, lack of knowledge of natural behaviour prevents informed speculation on the evolutionary origin of their intellectual abilities.

#### What Cognitive Mechanisms Does Social Intelligence Need?

‘Greater intelligence’ and ‘advanced cognition’ are terms used freely in discussions of sociality and brain

enlargement: but to a large extent they function as hedges, avoiding commitment to which particular cognitive mechanisms the animals in question are displaying. Without cooperative subjects under verbal instruction in a cognitive psychology laboratory, it may indeed be very hard to say; but in this final section we make an attempt to sketch what cognitive mechanisms are minimally implied by the data on social intelligence. The enterprise would be aided by a more sophisticated approach to understanding the mental processes involved in complex behaviour, replacing the blanket approach of 'learning' by one in which the particular cognitive systems of different species are modelled [86], so that individual cognitive components can be compared across species: working memory, selective attention, episodic memory, anticipatory planning, and so on. At present, we must begin with a simpler question: how far can variation between species be understood in terms of worse/better, and at what point do we need to invoke a richer understanding of the organization of animal minds.

The fact that many data sets show a *continuous* range of differences, in brain size and in frequencies of cognitively impressive behaviour, points to cognitive enhancements that are 'more of the same', rather than re-organization of cognitive architecture or the introduction of entirely new systems.

The highly social animal will certainly require a discriminating perceptual system, in order to distinguish those subtle cues that enable many different individuals to be recognized, and to identify nuances of facial expression, body posture or vocal timbre that indicate mood and disposition [31,87]. Social perception includes the selective attention mechanisms that allow a sustained focus on key areas for picking up relevant information, and avoid distraction by irrelevance. We know from human experience how powerful this sort of perception can be, even applied to novel stimuli: for instance, researchers in one long-running study regularly recognize individually almost all individuals of a population of 1200 elephants. What we do not know is how 'costly' it is in brain tissue: but 'visual' processing takes up large areas of human cortex, extending far beyond the visual area of the occipital lobe, so this may have made a major contribution to brain enlargement [31]. Primates are specialized for vision, but in other highly social mammal groups different perceptual systems may dominate: most dramatically, sonar in toothed whales and bats.

In addition to perceptual specializations, the complexities of social living may require more powerful means to register and employ knowledge. Large-brained, Old World monkeys can learn about other's rank and kinship from third-party observations alone [88], and many instances of subtle social manipulation by deception must have required learning from rare, if not unique, past events [89,90]. Very rapid learning, at least in social situations, is therefore another aspect where brain enlargement may increase efficiency of a primitive ability of all vertebrates. Moreover, knowledge about a substantial number of individuals, their typical interactions, and the history of who can be relied upon, must be learned from past events in order to respond appropriately in social interactions

within a large monkey group (or, presumably, a higher-order dolphin alliance, or a wild dog pack), or to 'network' within a social milieu made of many alliances. This would not be possible with a long-term memory system that was circumscribed or inefficient.

As Sir Bob Geldoff famously remarked after the first Live Aid concert: "Is that it?" Well, for most animals, we suspect yes. It is tempting to describe the social manoeuvring of non-human primates — reconciliation, alliance formation, tactical deception, referential communication — in human-like terms, as if the animals construed their actions as we do, planned them in advance and understood their *modus operandi*. A closer look at what these social skills involve suggests otherwise. Enlargement of mammalian neocortex confers abilities of highly discriminating perception, rapid learning in social contexts, and efficient long-term memory. The great bulk of the 'smart' social tactics of non-human primates and other species can be understood solely in these terms [17,91]. Indeed, a great deal of everyday human cognition is entirely based on sophisticated perception, rapid learning and extensive memory, though we sometimes retrospectively glamorize our actions in more richly intentional terms [92].

Everyday human experience in the social realm, however, indicates that there is further to go. For instance, we can work out what someone is likely to do next, not just on the basis of their past history with us and their current demeanour, but by working out what they know and believe: 'social attribution', or 'theory of mind'. Whether any non-humans can do this remains somewhat controversial, not least because it is not entirely clear how we do it ourselves! A number of 'theory of mind' tests, devised with preverbal children in mind, have been 'passed' by (for instance) chimpanzees and corvids [67,93]. It can be argued, however, that much of our everyday social attribution is carried out by sophisticated, unconscious statistical extraction of overt but subtle information [94–96]. It may be that we only more rarely carry out mental deductions about others' minds, and that doing so entails much more 'work' cognitively and requires language. Much the same argument may be made in the physical realm, where the highly efficient use that some non-human animals make of the physical world — including tool use, tool making, and dealing with mechanical and gravitational forces — may at root be based on an unconscious, statistically derived understanding of the complex world they live in, rather than the kind of propositional knowledge that one learns in school science classes [97].

The \$64,000 question is probably: 'Can animals plan for the future?' It is not unthinkable that non-linguistic animals are locked into present perceptions and past memories, and that all their achievements are managed without their ever thinking about what happens next [98,99]. Finding out definitively, rather than 'failing to disprove the null hypothesis' of inability, is a tall order, especially so when it comes to social cognition. If crows, dolphins, chimpanzees or meercats contemplate tomorrow, and work out social strategies on the basis of these anticipations, they have no easy way to tell us. And indeed, if their companions' demeanour

or intervening events made their best-laid plans infeasible, the plans would no doubt be aborted: and observers would conclude that memory and perception were all that was determining their behaviour.

While the jury is firmly out on whether animals make *social* plans, it may be possible to make more progress in other realms. And, as we have seen, it is most likely that advanced cognition — even if it resulted from selection purely in the social realm — has domain-general effects, so we should look more widely. Travel, in a familiar but large-scale environment — an area that cannot be scoped from a single viewpoint — is intrinsically about the future: animals set off ‘towards’ places that cannot be seen, and will not be reached until time has passed. If it can be shown that they set off *with intent* to reach those places, then we can be sure they are able to plan in anticipation and conceive of absent things and future events.

Recent research has shown that some large-brained, Old World monkeys show just this kind of ability when choosing where to forage. Mangabeys take account of recent past weather when deciding when unripe figs may be worth revisiting. That is, when they come close to a tree that has previously not been a good source of food but showed promise, their decision to go for it or not depends on the weather of the last several days, not just the weather of the day in question [100]. Baboons take account of the likely risk of other troops exploiting their prized resources. They make sure they head first to distant foods that invite exploitation by competing groups even when it means by-passing perfectly good food of other kinds, food that they return to eat later in the day [101]. In both cases, the animals must be computing future events that might take place at out-of-sight locations, and taking decisions accordingly.

The food-caching of some corvid species provides another arena in which advance planning would pay, and scrub jays show caching tactics that serve to increase the likelihood that the cache will be undiscovered, but only if they themselves have experience of pilfering other birds’ caches [66]. Moreover, they cache food in places that anticipate their future needs and likely local shortage [102]. It is sometimes argued that ‘real’ anticipatory planning necessarily involves decision-making about a future in which the individual is in a different motivational state to its present one [98]. This seems to muddle cognitive skills with the occasion of their use, and moreover the conjecture is more-or-less untestable in natural environments; but perhaps the ability to imagine, specifically, one’s own future bodily state might be a uniquely human one? It is not. Under controlled captive conditions, scrub-jays preferentially cache food of a type that they will value highly in the future, even when their current motivation to eat that food is low [103]. At least some animals, therefore, may also be using anticipatory planning in their social strategizing [104]: perhaps future studies will be able to home in upon such skills, currently seen as the province only of humanity.

#### Future Directions

Comparative analysis of brains has advanced from using gross measures of total brain or major lobe

volume: it is now accepted that evolution has acted independently on coordinated, functional systems [31]. Comparative cognition needs to make a similar transition. Categories as broad as ‘learning speed’, ‘perceptual efficiency’, ‘memory capacity’ and ‘anticipatory planning’ are inherently unsuitable for comparing the details of cognitive ability between different species of animal: they reduce all differences to more/less, yes/no judgements, without helping to explain how the tasks are actually performed. Within closely related groups of animals, or in species with limited, primitive abilities, it has been possible to finesse the details of information processing and thus use continuous measures of ‘ability’ to evaluate evolutionary theories. To go further in understanding those abilities, and especially when attempting to understand the advanced cognition that has arisen in widely-divergent groups of animal — primates, dolphins, parrots, crows — it becomes necessary to build theoretical models of the abilities themselves.

Animal learning theory has proceeded independently from human psychology for the last four decades [105], unaffected by the ‘cognitive revolution’. Learning theorists remain deeply reluctant to proliferate intervening variables if ‘association’ can be invoked, yet are little concerned at the explanatory adequacy of their theories. Notoriously, broad appeals to association learning are liable to lack adequacy as working explanations [106]. Precise models of information processing *can* be posed in terms of associations and tested in carefully controlled conditions. However, only quite simple situations can be examined in this way, meaning that ‘animal cognition’ risks always being seen as concerning the simple, unlike the rich complexity of human abilities. If we are instead to begin to understand the evolutionary origins of that human intelligence, it will be necessary to evaluate data from the inconveniently messy environments in which animals evolved — in the same terms as data from the neat world of the laboratory. Modelling abilities in cognitive terms, rather than as a mass of associations, allows testable models of process to be constructed relatively easily even in complex situations [86], making that more likely to happen.

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