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Introduction

Animal minds: from computation to evolution

1. INTRODUCTION

In the great Darwinian struggle for existence, all animals must tackle the problems posed by variable environments, be it finding and processing food, recognizing and attracting potential mates, avoiding predators, outcompeting rivals or navigating back to nesting sites. Although the mental processes by which different species deal with such challenges are varied, all animals share the fundamental problem of having to cope with the sheer abundance of information in the environment, much of which is likely to be irrelevant to the task at hand. The first step, therefore, is to attempt to sift through the mass of data and attend to that which may inform adaptive decision-making. Having acquired the relevant data, animals may then benefit from establishing how the different pieces of information relate to one another. Do yellow flowers reliably indicate the presence of nectar? Does the presence of a dominant silverback male signal impending danger? In complex environments, it may be advantageous not only to take into account statistical co-occurrence of different stimuli, but also to extract general rules, making it possible to act flexibly and solve a wide variety of problems across different contexts [1,2]. Certain animal species might also form mental representations or models of the way the world works. These internal representations may be used to reason about the desirability of alternative actions or scenarios, based on expectations of their likely outcome, thus guiding the individual's behaviour [3,4]. Thus, for instance, an animal with a mental representation of the action of gravity on objects could use it to reason that a food item will fall out of its reach if pushed towards a precipice [5,6]. The possibility that animals may employ such human-like reasoning has intrigued observers throughout the centuries, from Aesop's fables to Romanes's anthropomorphic anecdotes. However, careful scientific exploration of the mental faculties of other animals, and their relation to our own, did not commence in earnest until the past century, with the rise of comparative psychology and ethology. Contemporary comparative cognition, which grew from these two disciplines, aims to determine the mental processes underpinning animal behaviour, and to understand how these processes have evolved over the generations and develop over an animal's lifetime.

Recent years have seen a great burgeoning of studies of comparative cognition, building on earlier advances in our understanding of basic processes of perception, attention, associative learning and memory [4,7]. Elegant experimental work is generating insights into disparate cognitive abilities across a wide range of taxa, from path integration in ants and spatial memory in rats [8,9] to mental faculties that were considered uniquely human, such as mental state attribution and mental time travel in apes and corvids [10–13]. Nevertheless, despite these important empirical advances, the field suffers from a lack of theoretical underpinning, and conceptual debates abound. For example, how might we discriminate between alternative cognitive mechanisms underpinning behaviour? Do the abilities seen in cognitive experiments reflect domain-specific 'adaptive specializations' or domain-general problem-solving capacities? How and why do humans differ cognitively from other animals? This special issue brings together a variety of developmental, mechanistic and functional approaches to the study of cognition with the goal of synthesizing this emerging body of work, and beginning to build a theoretical framework to facilitate further progress towards our understanding of animal minds.

2. DELVING INTO ANIMAL MINDS: DETERMINING MECHANISMS OF ANIMAL COGNITION

The range of possible mental processes through which animals may interact with their environments poses a major challenge to students of animal minds. We can observe a non-verbal creature solving a problem, but how can we infer the processes by which it does so? This issue is particularly problematic given that seemingly complex behaviour may often be generated through relatively simple mechanisms. Meerkats, for instance, teach their young to hunt by responding to age-related changes in pups' begging calls, provisioning dead or disabled prey to young pups and live prey to older pups. A simple stimulus–response mechanism thus allows adults to provide pups with prey-handling opportunities appropriate for the pups' age and competence, without needing theory of mind to attribute ignorance to their pupils [14]. Similarly, reflexive responses coupled with associative learning processes enable many animals, from insects to primates, to use tools effectively without understanding their physical properties. For example, larval antlions (*Myrmeleon* spp.), insects of the order Neuroptera, knock passing prey into their pit-traps

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One contribution of 14 to a Discussion Meeting Issue 'Animal minds: from computation to evolution'.

by flinging grains of sand in response to vibrational cues [15]. How might we discriminate between such low-level mechanisms and other, more complex cognitive processes? It may be tempting to assume that species that are more closely related to us may share more 'human-like' cognitive faculties. However, numerous examples of evolutionary convergence in unrelated taxa, along with abundant evidence of the importance of relatively simple, evolutionarily ancient mental processes in human behaviour [16–18] caution against this archaic view of a mental *scala naturae*. Instead, the contributors to this volume urge a more careful, bottom-up approach to determine the minimal computational requirements needed to generate particular behavioural outcomes and to use careful experimentation to tease apart alternative explanations.

(a) *Bottom-up approaches: building models and robots*

It is common in comparative cognition to use folk psychological intuitions of how humans solve certain problems when designing experiments to test the cognitive abilities of other animals. While this approach has clear value in helping to derive hypotheses, it suffers from two major weaknesses. First, our intuitions of how we solve problems have repeatedly been shown not to reflect psychological reality [19,20]. Second, a reliance on folk psychological intuitions may detract from considering other, arguably more 'killjoy' explanations based on simpler mechanisms [17,18]. A fundamentally different approach advocated by some of the contributors to this issue is to build models of simple neural networks to determine the minimal necessary requirements to solve a specific task. These models often yield rather surprising results, suggesting that abilities that are commonly considered to be complex may in fact be implemented by very simple networks (see Chittka *et al.* [21]). A circuit of only a few hundred neurons, for example, has been shown to suffice for reliable face recognition [22]. This approach is clearly of great value in quantifying basic computational complexity, undermining the assumption that many cognitive feats require big brains [21,23]. Indeed, recent studies have revealed a number of striking cognitive feats in small-brained animals such as insects and, as Webb [3] discusses, there is evidence that insects may employ internal mental representations of the outside world. However, given that even miniscule invertebrate brains contain more neurons than the theoretical neural thresholds predicted by computational models for many tasks, this 'minimal cognition' approach may be limited in explaining observed cognitive differences between species. Moreover, the computational requirements for solving a specific, isolated problem may underestimate those needed to solve the same task in the real world, let alone solve multiple different tasks using the same network. One way to build up complexity towards that faced by an animal in the physical world is to build a robot that must replicate the animal's behaviour using the hypothesized neural mechanism to solve a given task. As Webb points out, robotics thus forces us to face real-world difficulties such as perceiving and attending to relevant stimuli in addition to the abstract computational aspects of a problem, thus generating more realistic demonstrations of minimal sufficiency. For example, a robotic female cricket may be able to discriminate between male songs and approach only those who sound like members of a given species without needing to rely on an internal computational mechanism for evaluating and comparing songs [3]. Unlike a real cricket, however, it cannot deal with the additional complexities involved in finding food and avoiding predators. The development of ever more complex robots, capable of computing solutions to multiple problems, may generate important insights into the computational requirements needed for biological systems to respond adaptively to the multitude of challenges they face in their natural environments. A related challenge is to determine how organisms may integrate currently available information with previously acquired knowledge of how the world works, bringing all the necessary cognitive resources to bear when faced with a novel problem. How are parallel processing units in the brain integrated to create a coherent, structured system capable of responding appropriately when encountering a problem for the first time? How might a New Caledonian crow (*Corvus moneduloides*) or a rook (*Corvus frugilegus*), for example, have the wherewithal to spontaneously manufacture a hook to pull up a bucket containing food [24,25]? Shanahan [26] takes a bottom-up approach, drawing on recent advances in brain connectivity to propose a cognitive architecture that can generate such seemingly insightful solutions to novel problems in the physical world. This consists of a number of discrete modules with extensive internal connectivity (a 'modular small-world network'), which are, in turn, connected to one another through nodes known as connector hubs to form a 'connective core'. Such a system may enable the unanticipated integration of mental processes to produce a coherent sequence of actions to achieve a goal. This theoretical approach thus holds the great promise of allowing us to move beyond current vague conceptions of insight as a sudden, magical 'Eureka moment', into a tangible computational process that is amenable to research. An important question arising from this work is how and why, given that the brains of humans, macaques, cats and pigeons are all known to possess a connective core, these species may nevertheless differ radically in their ability to plan their actions when solving a task. Answers to this question will emerge from a more detailed understanding of differences in neural connectivity in the brains of different species and their resulting computational power, coupled with the behavioural tests of the capability of different animals.

(b) *Top-down approaches: inferring cognitive mechanisms from behaviour*

(i) *Associative learning as a candidate explanation*

For behavioural researchers, a principal challenge is to devise experiments capable of discriminating between alternative mechanistic explanations for observed behaviour. The bottom-up approach exemplified by neural network models using computer simulations and robotics cannot yet provide testable predictions for the range of behaviours examined in contemporary comparative cognition research. Learning theory, in contrast, is grounded in behavioural research and provides concrete hypotheses that can be readily examined by empiricists. Indeed, associative learning is found throughout the animal kingdom and is known to play a role in generating even seemingly complex behaviour in both non-human animals and in our own species. Nevertheless, associative explanations are sometimes overlooked, perhaps as a result of knee-jerk reactions to the overambitious claims of behaviourism, leading to a focus on what Heyes [17] calls 'super-cognitive' explanations derived from folk psychological intuitions. In fact, modern learning theory is considerably more nuanced than the caricature of behaviourism would suggest. Unlike behaviourism, it does not claim that anything can be learned (or that all behaviour is learned), but instead incorporates constraints that limit learning of coincidental associations and promote learning of biologically relevant associations. Moreover, learning theory has the distinct advantage over folk psychology in that it rests on well-described, general theories such as the Rescorla–Wagner [27] and Mackintosh [28] models. One interesting development discussed by Dickinson [29] is his 'associative-cybernetic' theory [30,31], which postulates that, if embedded in a constraining processing architecture, associative learning may give rise to rational goal-directed action. That is, rather than simply learning that a certain action is rewarded, an animal may also learn that its action causes a specific, beneficial outcome. This theoretical prediction has considerable empirical support. For example, rats trained to obtain a reward by pressing a lever will reduce their lever pressing if the value of the reward is reduced, indicating that they represent the causal relation between their own lever-pressing actions and the outcome (reviewed in Dickinson [29]). Thus, associative learning theory provides a powerful and tractable framework for research on animal (including human) minds. Indeed, rigorous research in comparative cognition often uses associative learning as a null hypothesis, making considerable efforts to derive candidate explanations from learning theory to be tested through behavioural experiments [32]. There will, of course, be instances when behaviour cannot be understood purely in terms of associative processes. Human behaviour, for instance, is guided to a large extent by reasoning and inference about abstract causal relations in the physical and social worlds [33–35]. The possibility that animals may employ similar cognitive processes has attracted a great interest from students of animal minds, but lacks the theoretical grounding of associative theory and so is more difficult to pin down. If associative processes are found to be lacking as explanations of animal behaviour, how might we make progress in determining alternatives?

(ii) *Beyond associative learning: individual-level approaches*

One common and powerful experimental approach is to use a series of training trials in which subjects learn the basic requirements of the task, followed by transfer tests in which the causal properties of the problem are kept constant, but arbitrary visible stimuli are changed. Thus, in theory, subjects that have learned a simple rule based on visible features will fail transfers, while those that have abstracted a generalizable understanding of the causal structure of the task should apply it to solve the transfer [36,37]. However, as Thornton & Lukas [38] point out, the fact that transfer tests typically involve the same binary choice over multiple trials means that a subject might learn a rule based on the visible properties of the transfer test itself. Thus, subjects may reach a given criterion (say nine correct trials out of ten) using nothing but associatively learned rules. Conversely, reliance on crude binary criteria of success or failure leads us to ignore potentially valuable data. Instead, several of the contributors to this issue advocate a more fine-grained analytical approach that focuses specifically on individual differences in performance on a trial-by-trial basis to shed light on the cognitive mechanisms employed when solving tasks [33,38,39]. Seed and co-workers, drawing on insights from developmental psychology, point out that a detailed focus on individual behaviour, taking into account failed trials as well as successes, may provide valuable insights into why subjects may fail, and the precise mechanisms required for success. By using this approach, they show that chimpanzees (*Pan troglodytes*) that failed a task requiring them to discriminate between a complete and a broken tool failed not because of an inability to represent 'connectedness' but rather because of limitations in memory and attention [33]. Thus, an individual-based analytical approach may allow us to determine the set of cognitive processes that must be employed together when solving tasks.

The individual-level approach may also benefit from using formal planning theory used in artificial intelligence (AI) research. In this issue, Chappell & Hawes explored a four-trap variant of the classic 'trap tube' test in which the precise characteristics of the task (e.g. which of the four traps was functional) varied systematically across a series of 64 trials. Using an AI planning language, they generated a series of possible computational rules or 'plans' an animal could employ to solve the task. They then simulated how each of these plans would perform in each of the different trials, and compared these simulations with the actual trial-by-trial performance of orangutans (*Pongo pygmaeus*) [39]. The advantage of this method is twofold. First, decomposing the problem into its constituent parts may be valuable in designing experiments. Second, in common with Seed *et al.*'s approach, it forces us to move away from the simplistic and statistically problematic [38] dichotomy of success and failure and instead to harness the rich data emerging from all the actions of all individuals in all trials to assess how animals solve problems. In future, we hope that such individual-based approaches will be combined with insights from learning theory to determine the role of associative processes in within-task learning, and to discriminate between alternative mechanistic explanations. We also envisage a great potential in linking this top-down approach of decomposing and simplifying specified problems with bottom-up approaches that specify the components and connectivity of the computational systems implementing the solutions. For instance, specifying the computational components and connectivity of a neural system (cf. [26]) may allow us to constrain the possible range of plans the system might implement to solve a cognitively challenging task in a biologically realistic way.

3. THE EVOLUTION OF ANIMAL MINDS

(a) *Fitness consequences of individual cognitive variation*

Through a combination of experimental and theoretical approaches, comparative cognition is beginning to provide important insights into the mental processes of different animals. However, existing approaches tend to place relatively little emphasis on the central goal of understanding how these processes evolve. In this issue, Thornton & Lukas point out that researchers commonly assume that the cognitive traits they find in laboratory animals are the adaptive products of natural selection, but they very seldom assess whether the basic tenets of Darwinian theory apply to the trait in question [38]. For natural selection to act, there must be heritable variation in the trait, leading to variation in reproductive success [40]. Consequently, if we want to understand how cognitive traits evolve, we must ask whether they vary between individuals, are heritable and influence fitness. Laboratory studies commonly reveal substantial variation in individual performance, but rarely consider its causes. Thornton & Lukas's meta-analyses of individual performance across a series of cognitive tasks suggest that much of this variation may be explained by laboratory rearing conditions, with enculturated individuals with extensive previous experience of laboratory tests typically outperforming the rest [38]. It is therefore unclear to what extent this variation may be heritable, or indeed how cognitive traits may be manifested in the natural conditions in which they evolved. In some short-lived animals, it may be possible to explore cognitive evolution using selection experiments in the laboratory [41], but for many of the birds and mammals of interest to students of comparative cognition, such experiments are less feasible. Laboratory studies must therefore be complemented by field research to examine links between individual cognitive variation and reproductive fitness. Unfortunately, the difficulties in examining cognition in the wild have led to a recent trend for field researchers to assume that individuals that succeed in any experimentally presented 'problem-solving task' possess elevated cognitive abilities, without testing the underlying mechanisms. Given this trend, there is a danger that, for example, the action of a pigeon pecking a key to obtain a reward in the field would be regarded as a measure of 'cognition', while no one would consider the same action to be cognitive if done in a laboratory setting. If field studies are to provide productive insights into cognitive evolution, it is therefore critical that they incorporate the valuable lessons of psychological research concerning cognitive mechanisms into the task design. For instance, Visalberghi *et al.* [42] have used elegant experiments inspired by laboratory tests of physical cognition to establish that capuchin monkeys recognize the physical properties that render objects suitable for use as hammers to crack nuts. Similarly, studies by Healy and colleagues have elegantly adapted laboratory tests of spatial memory and timing for use in the field (reviewed by Healy *et al.* [43]), while Cheney & Seyfarth [44] and McComb & co-workers [45] have devised tests of social cognition incorporating expectation violation paradigms from developmental psychology. Such experimental approaches, as well as novel statistical tools allowing mechanisms of learning and cognition to be inferred from natural behaviour [46], hold great promise in enabling us to understand the cognitive processes used by animals in their environments. A key challenge now is to determine whether individual animals in the wild vary in their cognitive abilities, to use advances in quantitative genetics to assess the heritability of this variation and to begin to examine its fitness consequences.

It may be tempting to assume that elevated cognitive abilities ought always to confer fitness benefits, and are therefore subject to positive selection. However, any benefits associated with improvements in cognition will be balanced against the costs they may carry. In *Drosophila*, for example, there is evidence that selection for improved associative learning abilities among adults comes at a cost of reduced ability to compete for food resources at the larval stage [47]. In addition, at the individual-level, the potential benefits of cognition will depend on behavioural phenotypes. As Sih & del Giudice [48] discuss, there is extensive evidence that individual animals differ consistently in their behaviour over time and across contexts, and this behavioural consistency may place important constraints on the ways in which cognitive abilities are manifested. Consider, for example, two individuals that have equal cognitive abilities but differ in their behaviour, with one being very bold and exploratory while the other is shy and slow to investigate unknown places or objects. While the bolder individual is likely to encounter novel stimuli more often, the shier individual may have a greater tendency to pause and attend to changes in the environment and update its assessment of a given situation. Behavioural differences may therefore generate a trade-off between speed and accuracy when dealing with novel problems, and influence the benefits that individuals can derive from their cognitive abilities.

Just as individuals commonly exhibit suites of intercorrelated behaviours (termed 'behavioural syndromes' [48]), they may also exhibit consistency in cognitive abilities across different contexts. Indeed, there is a longstanding debate as to whether animal behaviour is underpinned by cognitive specializations that have evolved to fulfil specific ecological functions (e.g. retrieving cached food [49–51]), or rather is governed by domain-general mechanisms that operate across contexts. Herrmann & Call [52], using large datasets of the individual cognitive performance of chimpanzees across a test battery of multiple different tasks, suggest that the truth may lie somewhere in between the two views. Their analyses reveal that while some exceptional chimpanzees consistently outperformed their conspecifics across a range of tasks, there is no evidence for one single 'general intelligence' factor, but neither were performances entirely unrelated across different tasks. Rather, the data appear to support the existence of a number of distinct clusters of abilities, such as spatial knowledge and discrimination learning [52]. Further work is needed to determine whether the cognitive abilities of other organisms will exhibit similar clustering, but the evidence from chimpanzees suggests that there may be common mechanisms that animals apply to different tasks within particular clusters of abilities. An understanding of cognitive evolution will therefore benefit from explicit theoretical models to consider not only how overt, measurable behavioural abilities evolve, but also how selection may act on the underlying mechanisms [53].

(b) *Modelling the evolution of cognitive mechanisms*

As Lotem & Halpern [54] discuss, rigorous theoretical analyses of cognitive evolution must consider how different components of cognitive processing interact and coevolve. For example, to understand how learning mechanisms evolve, we must also consider the evolution of attentional and motivational mechanisms. Although traditional learning models assume that data are presented to the animal as discrete, distinguishable stimuli, Lotem & Halpern's model explicitly considers the fact that animals must sift through and obtain relevant information from the morass of data in their environments. The model assumes that, when animals encounter biologically relevant stimuli such as food, they will also attend to other information in the immediate environment. This array of data is then compared with previously encountered datasets. Segments of data that are rarely encountered tend to be forgotten and decay, while links between commonly encountered segments increase in weight and may become fixed in memory. Thus, by segmenting and linking chunks of data according to encounter rates and allowing irrelevant data to decay, the animal may build up a structured representation of the environment without the heavy computational burden of learning and remembering connections between all possible segments of data. Natural selection may act to tweak the parameters of both the data acquisition and learning mechanisms, resulting in organisms that are well adapted to handle the natural distribution of biologically relevant data in their environment. Lotem & Halpern argue that this process of coevolution of data acquisition and learning may generate incremental cognitive change, allowing organisms to extract relevant data even when faced with dynamic and complex arrays of information such as those that characterize some social systems. In their view, this process might even facilitate key human cognitive characteristics such as theory of mind and language acquisition [54–56].

4. THE QUESTION OF HUMAN UNIQUENESS

Of course, the quest to understand how and why the cognitive abilities of our own species may differ from those of other animals has long been a central motivating force for much of comparative cognition. What cognitive processes make us unique, and what are the origins of these processes? As Shettleworth [57] discusses in her contribution to this issue, there have been a multitude of theories of human uniqueness throughout the years. Some of these suggest that the difference between humans and other animals lies in broad, domain-general processes that are manifested across a wide range of behavioural contexts [58,59]. In contrast, evolutionary psychologists have tended to view human cognition as comprising a suite of discrete modules, some of which may exist in our species alone [60]. Both of these approaches appear to emphasize dichotomous distinctions between 'us and them'. Is a given cognitive faculty (be it domain-general or specific) uniquely human, or might it be found in other animals? Such human versus non-human comparisons suffer from two main problems. First, comparative studies have tended to apply tests designed for adult, verbal humans and thus may often risk underestimating the abilities of non-verbal creatures [61]. Second, an emphasis on the presence or absence of particular cognitive capacities may detract attention from the possibility that, even if an animal fails a test of some human ability, some of the cognitive processes it applies may still be shared with humans. Instead, Shettleworth [57] and Spelke & Lee [35] argue that important insights may lie in examining the development of cognitive abilities over individual lifetimes. Just as evolutionary biologists recognize that seemingly different traits may share important developmental commonalities [62], it is increasingly clear that comparisons of developmental cognitive trajectories may also reveal important elements of similarity and difference between species. For example, experiments by Spelke & Lee [35] suggest that human spatial cognition develops in two distinct stages. From infancy, children exhibit two systems for representing objects and vectors. These are largely shared with other animals and are thus likely to be evolutionarily ancient cognitive adaptations for navigation. Later in development, the acquisition of language and culture enables children to combine the two systems in uniquely human ways to form abstract geometrical concepts (reviewed in Spelke & Lee [35]). Tomasello, Call and colleagues place a similar emphasis on developmental processes as being at the heart of human socio-cognitive uniqueness (reviewed in Tomasello [63]). Their extensive comparative experiments suggest that while human children and apes show similar performance on tests of physical, spatial and numerical cognition, children typically outperform apes on social tasks. In particular, they argue that, unlike our closest relatives, humans are endowed from an early age with the motivation to engage with others in joint activities involving shared goals and attention. Later in development, this tendency facilitates the use of linguistic symbols and the creation of cultural norms [52,64,65]. As these examples show, a continued emphasis on developmental processes in comparative cognition is likely to yield further important insights into the similarities and differences between humans and other species. To fully take advantage of this approach, it is important to extend the current focus on comparing children with adult non-human animals to compare developmental trajectories across species, acknowledging the fact that non-human cognition also develops. Indeed, a common theme of this issue is that, as the field of comparative cognition matures, it must incorporate careful comparative analyses across all levels—within individual lifetimes, between individuals and between species. Understanding animal cognition is a deeply challenging endeavour, not least because it requires investigation of multiple layers, from genes and neurons to computational processes and the resulting behaviours to the developmental and evolutionary processes shaping cognition over time. We hope that a synthesis of empirical and theoretical tools from fields including robotics, neuroscience, psychology and biology, such as those showcased in this issue, will help future research further unravel the mysteries of animal minds.

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REFERENCES

1 Murphy, R. A., Mondragón, E. & Murphy, V. A. 2008 Rule learning by rats. *Science* **319**, 1849–1851. (doi:10.1126/science.1151564)

2 Wilson, B., Mackintosh, N. J. & Boakes, R. A. 1985 Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Q. J. Exp. Psychol. B* **37**, 313–332. (doi:10.1080/14640748508401173)

3 Webb, B. 2012 Cognition in insects. *Phil. Trans. R. Soc. B* **367**, 2715–2722. (doi:10.1098/rstb.2012.0218)

4 Pearce, J. M. 2008 *Animal learning and cognition: an introduction*, 3rd edn. New York, NY: Psychology Press.

5 Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S. 2006 Investigating physical cognition in rooks, *Corvus frugilegus*. *Curr. Biol.* **16**, 697–701. (doi:10.1016/j.cub.2006.02.066)

6 Hood, B. M., Hauser, M. D., Anderson, L. & Santos, L. 1999 Gravity biases in a non-human primate? *Dev. Sci.* **2**, 35–41. (doi:10.1111/1467-7687.00051)

7 Shettleworth, S. J. 2010 *Cognition, evolution and behaviour*, 2nd edn. Oxford, UK: Oxford University Press.

8 Broadbent, N. J., Squire, L. R. & Clark, R. E. 2004 Spatial memory, recognition memory, and the hippocampus. *Proc. Natl Acad. Sci. USA* **101**, 14 515–14 520. (doi:10.1073/pnas.0406344101)

9 Muller, M. & Wehner, R. 1988 Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl Acad. Sci. USA* **85**, 5287–5290. (doi:10.1073/pnas.85.14.5287)

10 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)

11 Clayton, N. S. & Dickinson, A. 1998 Episodic-like memory during cache recovery by scrub jays. *Nature* **395**, 272–274. (doi:10.1038/26216)

12 Call, J. & Tomasello, M. 2008 Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* **12**, 187–192. (doi:10.1016/j.tics.2008.02.010)

13 Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007 Planning for the future by western scrub-jays. *Nature* **445**, 919–921. (doi:10.1038/nature05575)

14 Thornton, A. & McAuliffe, K. 2006 Teaching in wild meerkats. *Science* **313**, 227–229. (doi:10.1126/science.1128727)

15 Devetak, D. 1998 Detection of substrate vibration in Neuropteriodea: a review. *Acta Zool. Fennica* **209**, 87–94.

16 Seed, A. M., Emery, N. J. & Clayton, N. S. 2009 Intelligence in corvids and apes: a case of convergent evolution? *Ethology* **115**, 401–420. (doi:10.1111/j.1439-0310.2009.01644.x)

17 Heyes, C. 2012 Simple minds: a qualified defence of associative learning. *Phil. Trans. R. Soc. B* **367**, 2695–2703. (doi:10.1098/rstb.2012.0217)

18 Shettleworth, S. J. 2010 Clever animals and killjoy explanations in comparative psychology. *Trends Cogn. Sci.* **14**, 477–481. (doi:10.1016/j.tics.2010.07.002)

19 Gigerenzer, G. 1999 *Simple heuristics that make us smart*. Oxford, UK: Oxford University Press.

20 Silva, F. J., Page, D. M. & Silva, K. M. 2005 Methodological-conceptual problems in the study of chimpanzees' folk physics: how studies with adult humans can help. *Learn. Behav.* **33**, 47–58. (doi:10.3758/BF03196049)

21 Chittka, L., Rossiter, S. J., Skorupski, P. & Fernando, C. 2012 What is comparable in comparative cognition? *Phil. Trans. R. Soc. B* **367**, 2677–2685. (doi:10.1098/rstb.2012.0215)

22 Strausfeld, N. J. 2009 Brain organization and the origin of insects: an assessment. *Proc. R. Soc. B* **276**, 1929–1937. (doi:10.1098/rspb.2008.1471)

23 Chittka, L. & Niven, J. 2009 Are bigger brains better? *Curr. Biol.* **19**, R995–R1008. (doi:10.1016/j.cub.2009.08.023)

24 Bird, C. D. & Emery, N. J. 2009 Insightful problem solving and creative tool modification by captive non-tool-using rooks. *Proc. Natl Acad. Sci. USA* **106**, 10 370–10 375. (doi:10.1073/pnas.0901008106)

25 Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002 Shaping of hooks in New Caledonian crows. *Science* **297**, 981. (doi:10.1126/science.1073433)

26 Shanahan, M. 2012 The brain's connective core and its role in animal cognition. *Phil. Trans. R. Soc. B* **367**, 2704–2714. (doi:10.1098/rstb.2012.0128)

27 Rescorla, R. & Wagner, A. 1972 Variations in the effectiveness of reinforcement and nonreinforcement. In *Classical conditioning II: current research and theory* (eds A. H. Black & W. F. Prokasy), pp. 64–99. New York, NY: Appleton-Century-Crofts.

28 Mackintosh, N. J. 1974 *The psychology of animal learning*. New York, NY: Academic Press.

29 Dickinson, A. 2012 Associative learning and animal cognition. *Phil. Trans. R. Soc. B* **367**, 2733–2742. (doi:10.1098/rstb.2012.0220)

30 de Wit, S. & Dickinson, A. 2009 Associative theories of goal-directed behaviour: a case for animal-human translational models. *Psychol. Res.* **73**, 463–476. (doi:10.1007/s00426-009-0230-6)

31 Dickinson, A. 1994 Instrumental conditioning. In *Animal learning and cognition* (ed. N. J. Mackintosh), pp. 45–79. San Diego, CA: Academic Press.

32 Clayton, N. S. & Dickinson, A. 1999 Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *J. Exp. Psychol.* **25**, 82–91.

33 Seed, A. M., Seddon, E., Greene, B. & Call, J. 2012 Chimpanzee 'folk physics': bringing failures into focus. *Phil. Trans. R. Soc. B* **367**, 2743–2752. (doi:10.1098/rstb.2012.0222)

34 Penn, D. C. & Povinelli, D. J. 2007 Causal cognition in human and nonhuman animals: a comparative, critical review. *Annu. Rev. Psychol.* **58**, 97–118. (doi:10.1146/annurev.psych.58.110405.085555)

35 Spelke, E. S. & Lee, S. A. 2012 Core systems of geometry in animal minds. *Phil. Trans. R. Soc. B* **367**, 2784–2793. (doi:10.1098/rstb.2012.0210)

36 Heyes, C. M. 1993 Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Anim. Behav.* **46**, 177–188. (doi:10.1006/anbe.1993.1173)

37 Heyes, C. M. 1998 Theory of mind in nonhuman primates. *Behav. Brain Sci.* **21**, 101–134. (doi:10.1017/S0140525X98000703)

38 Thornton, A. & Lukas, D. 2012 Individual variation in cognitive performance: developmental and evolutionary perspectives. *Phil. Trans. R. Soc. B* **367**, 2773–2783. (doi:10.1098/rstb.2012.0214)

39 Chappell, J. & Hawes, N. 2012 Biological and artificial cognition: what can we learn about mechanisms by modelling physical cognition problems using artificial intelligence planning techniques? *Phil. Trans. R. Soc. B* **367**, 2723–2732. (doi:10.1098/rstb.2012.0221)

40 Darwin, C. 1859 *On the origin of the species by means of natural selection*. London, UK: John Murray.

41 Dukas, R. 2004 Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Evol. Syst.* **35**, 347–374. (doi:10.1146/annurev.ecolsys.35.112202.130152)

42 Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. 2009 Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.* **19**, 213–217. (doi:10.1016/j.cub.2008.11.064)

43 Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P. & Kelley, L. A. 2009 Explanations for variation in cognitive ability: behavioural ecology meets comparative cognition. *Behav. Proc.* **80**, 288–294. (doi:10.1016/j.beproc.2008.10.002)

44 Cheney, D. L. & Seyfarth, R. M. 2007 *Baboon metaphysics: the evolution of a social mind*. Chicago, IL: University of Chicago Press.

45 Proops, L., McComb, K. & Reby, D. 2009 Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proc. Natl Acad. Sci. USA* **106**, 947–951. (doi:10.1073/pnas.0809127105)

46 Hoppitt, W. J. E., Samson, J., Laland, K. N. & Thornton, A. 2012 Identification of learning mechanisms in a wild meerkat population. *PLoS ONE* **7**, e42044. (doi:10.1371/journal.pone.0042044)

47 Mery, F. & Kawecki, T. J. 2003 A fitness cost of learning ability in *Drosophila melanogaster*. *Proc. R. Soc. Lond. B* **270**, 2465–2469. (doi:10.1098/rspb.2003.2548)

48 Sih, A. & Del Giudice, M. 2012 Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Phil. Trans. R. Soc. B* **367**, 2762–2772. (doi:10.1098/rstb.2012.0216)

49 Healy, S. D., de Kort, S. R. & Clayton, N. S. 2005 The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends Ecol. Evol.* **20**, 17–22. (doi:10.1016/j.tree.2004.10.006)

50 Dwyer, D. M. & Clayton, N. S. 2002 A reply to the defenders of the faith. *Trends Cogn. Sci.* **6**, 109–111. (doi:10.1016/S1364-6613(00)01857-X)

51 Bolhuis, J. J. & Macphail, E. M. 2001 A critique of the neuroecology of learning and memory. *Trends Cogn. Sci.* **5**, 426–433. (doi:10.1016/S1364-6613(00)01753-8)

52 Herrmann, E. & Call, J. 2012 Are there geniuses among the apes? *Phil. Trans. R. Soc. B* **367**, 2753–2761. (doi:10.1098/rstb.2012.0191)

53 McNamara, J. M. & Houston, A. I. 2009 Integrating function and mechanism. *Trends Ecol. Evol.* **24**, 670–675. (doi:10.1016/j.tree.2009.05.011)

54 Lotem, A. & Halpern, J. Y. 2012 Coevolution of learning and data-acquisition mechanisms: a model for cognitive evolution. *Phil. Trans. R. Soc. B* **367**, 2686–2694. (doi:10.1098/rstb.2012.0213)

55 Lotem, A. & Halpern, J. Y. 2008 A data-acquisition model for learning and cognitive development and its implications for autism. *Cornell computing and information science technical reports.* See http://hdl.handle.net/1813/10178.

56 Goldstein, M. H., Waterfall, H. R., Lotem, A., Halpern, J. Y., Schwade, J. A., Onnis, L. & Edelman, S. 2010 General cognitive principles for learning structure in time and space. *Trends Cogn. Sci.* **14**, 249–258. (doi:10.1016/j.tics.2010.02.004)

57 Shettleworth, S. J. 2012 Modularity, comparative cognition and human uniqueness. *Phil. Trans. R. Soc. B* **367**, 2794–2802. (doi:10.1098/rstb.2012.0211)

58 Penn, D. C., Holyoak, K. J. & Povinelli, D. J. 2008 Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* **31**, 109–130. (doi:10.1017/S0140525X08003543)

59 Suddendorf, T. & Corballis, M. C. 2007 The evolution of foresight: what is mental time travel, and is it unique to humans? *Behav. Brain Sci.* **30**, 299–313. (doi:10.1017/S0140525X07001975)

60 Cosmides, L., Barrett, H. C. & Tooby, J. 2010 Adaptive specializations, social exchange, and the evolution of human intelligence. *Proc. Natl Acad. Sci. USA* **107**, 9007–9014. (doi:10.1073/pnas.0914623107)

61 Boesch, C. 2007 What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *J. Comp. Psychol.* **121**, 227–240. (doi:10.1037/0735-7036.121.3.227)

62 Carroll, S. B. 2005 *Endless forms most beautiful*. New York, NY: WW Norton & Company.

63 Tomasello, M. 2009 *Why we cooperate*? Cambridge, MA: MIT Press.

64 Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–691. (doi:10.1017/S0140525X05000129)

65 Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B. & Tomasello, M. 2007 Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* **317**, 1360–1366. (doi:10.1126/science.1146282)