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Review

What is comparable in comparative cognition?

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To understand how complex, or ‘advanced’ various forms of cognition are, and to compare them between species for evolutionary studies, we need to understand the diversity of neural–computational mechanisms that may be involved, and to identify the genetic changes that are necessary to mediate changes in cognitive functions. The same overt cognitive capacity might be mediated by entirely different neural circuitries in different species, with a many-to-one mapping between behavioural routines, computations and their neural implementations. Comparative behavioural research needs to be complemented with a bottom-up approach in which neurobiological and molecular-genetic analyses allow pinpointing of underlying neural and genetic bases that constrain cognitive variation. Often, only very minor differences in circuitry might be needed to generate major shifts in cognitive functions and the possibility that cognitive traits arise by convergence or parallel evolution needs to be taken seriously. Hereditary variation in cognitive traits between individuals of a species might be extensive, and selection experiments on cognitive traits might be a useful avenue to explore how rapidly changes in cognitive abilities occur in the face of pertinent selection pressures.

Keywords: brain; convergent evolution; homology; intelligence; neural circuits

1. INTRODUCTION

The central goal of comparative cognition is, of course, to find out how cognition evolves. To this end, standard evolutionary tools are used—one maps traits onto established phylogenetic trees, and in this way infers homology, evolutionary ancestry of cognitive traits or evolutionary convergence [1]. We argue that many such studies in the past have applied a relatively restrictive top-down approach, where researchers sometimes set out to discover human-like behaviours in animals [2,3]. This approach is prone to terminological ambiguities, because terms taken from the domain of human experience often invoke more complex connotations than the restricted criteria used to test the phenomena in an experimental setting with animals would permit. It also bears the risk of circularities as a consequence of selecting and shaping definitions and test criteria [4]. Finally, a narrow top-down approach may be vulnerable to biases, such as to predominantly report positive results or to mainly investigate ‘clever’ animals [5]. A mechanistic, bottom-up approach is needed, with a focus on exploring the neural underpinnings of cognitive features, and the genes that control them [6–8]. This will be useful not only to quantify and

compare cognitive complexity, but also to explore the evolutionary background of cognitive traits. Contrary to the popular approach to dissect ‘why’ questions in biology into proximate and ultimate perspectives, we hold that questions about the evolution of behaviour and cognition are difficult to answer without an explanation of the mechanisms that are the basis of variation, not just the functions that are under selection.

In exploring whether non-human animals have consciousness, culture, theory of mind, for example, and to explore the evolutionary roots of these phenomena, many studies actually focus on whether behavioural feats conform to certain definitions, rather than explore whether these are based on comparable evolutionary features [7,9]. Concepts and terms are often borrowed from studies on human psychology, and then applied to other animals [2]. In the process, definitions are sometimes adjusted so that they can be applied to animals in meaningful ways—this is fine in principle, but the more permissive the definition, the more species will qualify, and the more examples of functional convergence (or indeed homology) we will find; in other words, the identification of evolutionary patterns in cognition will hinge, to some extent, on semantics, rather than actual biological traits. Given the many controversies about how to diagnose and define cognitive performance, this is surely an undesirable scenario.

In addition, one might argue that some of the most exciting discoveries about unique behaviour patterns

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would never have been made, had a strictly top-down, human-anchored approach been used throughout. Would Frisch [10] ever have discovered the bee 'dance language' had he deliberately set out to find a form of 'language' in the animal kingdom? Probably not—and in fact the question of definition—whether or not this symbolic communication warrants the term 'dance' or in fact a 'language'—is perhaps secondary to the fascination with the uniqueness of this communication system.

Even if we can agree on the definition of cognitive traits, the question remains whether behavioural performance can be compared in meaningful ways across species without a consideration of underlying mechanisms. For example, an analysis of colour learning speed in 11 animal species found honeybees to be the fastest at reaching a criterion, followed by fishes, then birds, and the slowest were human infants [11]. Curiously, this result, which runs counter to the accepted *scala naturae*, was then used to argue that learning speed is not a useful measure of intelligence! There may be good reasons not to equate learning speed with intelligence, but the fact that humans do not top the chart should not be one of them. The reason that honeybees perform well on colour learning tasks is that evolution has prepared them to memorize floral cues [12,13]. This complication—that a given task will often be closer to some species' natural biology than to some other species'—has led to the recommendation that cognition should be explored in tasks that are removed from those typically encountered in the animals' natural setting [14]. But, it appears almost impossible to rule out entirely that some animals will be better prepared to deal with certain laboratory tasks because they might be related, in subtle ways, to naturally relevant challenges. To compensate for such complications, some researchers have suggested that different taxa require adjustments in experimental techniques [15,16]. However, it is sometimes unclear whether this improves comparability of performance across species or eliminates it altogether.

An added complication is that negative results in comparative cognition are sometimes hard to interpret—did the animal fail the test because it really lacked an ability, or because inappropriate methods were employed [7]? There are many examples where negative results have been initially interpreted to mean that, for example, apes do not display imitation, theory of mind, or understand gravity, where subsequent work showed that, with adjusted procedures, animal subjects pass the grade after all [7,17]. One possible solution is to gradually increase task complexity until performance breaks down [18], but just as with our discussion of definitions above, there is some danger that we might adjust procedures or behavioural criteria until we find the desired phenomenon.

Finally, a complication in mapping overt behavioural abilities onto phylogenetic trees is that the same (or similar) sensory or cognitive feats might be generated by entirely different mechanisms that have arisen by convergent evolution [19]. On occasion, these are clearly identifiable as instances of convergence when abilities have emerged in highly distinct lineages, such as echolocation in bats and dolphins [20,21] or

flexible tool use in primates and corvids [22]. Yet, distinguishing homology from convergence is sometimes difficult without knowledge of the underlying mechanisms. Electrolocation in weakly electric fish arose independently in the South American and African lineages, where different areas of the brain mediate the analysis of electro-sensory input [23]. Examples of parallel evolution, where behavioural abilities arise independently from homologous structures or genes are also widespread [19,21], and these cases illustrate the difficulty in deducing homology or convergence from mere behavioural abilities even more strongly.

2. COMPARISONS OF GROSS NEUROANATOMY

The complications with using either brain size or gross anatomy as correlates of cognitive capacity are clear [4,24], so we will not dissect them here in detail. Without an exploration of internal neuronal wiring patterns, such analyses are unhelpful for comparative studies. There are now a number of very instructive studies where comparisons of cognitive abilities in different species are complemented with investigations of the underlying neural circuitry [7], where neurobiological work has indeed helped resolve controversies whether certain abilities can be said to exist in non-humans. For example, in studies on face recognition, imitation, prosocial behaviour and empathy, it appears that homologous cortical structures are recruited in humans and various primates when engaged in tasks related to these traits. Such results inspire some confidence in the fact that these behavioural phenomena (albeit tested somewhat differently in humans and non-humans) are comparable and homologous [7].

Features of gross brain anatomy can be well mapped onto phylogenies of various taxa [25,26], suggesting some phylogenetic constraints on brain evolvability [19]. On the other hand, it is not clear to what extent this constrains the evolution of cognitive capacity in the face of relevant selective pressures, or only insofar as evolution tends to proceed along similar paths with similar starting points when selection pressures are similar. For example, New World *Cebus* monkeys and Old World macaques have both evolved a high level of dexterity that is accompanied by parallel enlargements of homologous cortical areas involved in proprioception, motor planning and visually guided hand movements [27]. Song learning in birds has evolved at least twice by homologous anterior fore-brain regions convergently assuming similar functions [19]. Similarly, the independent evolution of high-duty cycle echolocation in unrelated lineages of Old World and New World bats—which enhances the ability to detect fluttering insects [28]—correlates with specializations in the cochlea and higher auditory centres [29]. Such examples suggest that evolution repeatedly proceeds along similar paths, perhaps where exapted circuits are well-preconfigured to produce novel behaviours when selection favours them.

Many impressive behavioural/cognitive capacities, while they clearly must have a neural substrate, are not readily detectable in terms of gross neuroanatomy. For example, one of the most impressive discoveries in insect social cognition in recent times was the

discovery of individual face recognition in Polistine wasps, and its role in social hierarchies [30]. Nonetheless, no discernable differences were found in the neuropiles of the visual systems of these remarkable wasps compared with related species in which face recognition does not occur [31]. Likewise, in an attempt to identify a neural correlate of the honeybee ‘dance language’, no ‘dance-specific’ sensory projections were found in the brains of honeybees when compared with other species that lack the dance [32]. The human brain, for all its obvious differences in cognitive output compared to other primates, appears, at least, in terms of coarse organization, in many respects to be a scaled-up version of the primate brain [7,33]. While there are certainly differences at the circuitry level, cortical modules once thought to be engaged in uniquely human functions (e.g. Broca’s and Wernicke’s areas) have clear homologues in other primates [34,35]. This emphasizes that even seemingly major evolutionary innovations relevant to behaviour and cognition might be generated by relatively small adjustments in neural circuitry that might be hard to detect by coarse-voxelled imaging studies or gross neuroanatomy.

3. COMPARISONS AT THE CIRCUITRY LEVEL

While we do not know the detailed neuron-to-neuron circuitry for any advanced cognitive function, it is clear that this has to be a desideratum to make meaningful comparisons between species. There are several lines of evidence that cognitive operations can be performed within fairly small circuits [36] and that therefore evolutionary shifts in cognitive capacity could be mediated by changes at the microcircuit level. One is that many ‘advanced’ cognitive capacities have recently been discovered in small brained animals such as insects (see [4,37,38] for reviews), and minimum circuitry models show that many such abilities could be mediated by very small neuron numbers and connections (see below). In addition, the widespread nature of the basic building blocks for cognition throughout the animal kingdom indicates that various forms of behavioural plasticity were, at least, in principle evolvable in some of the earliest animals. Almost all of the molecular components of nerve cells, i.e. ion channels, pumps, exchangers, neurotransmitters and G-protein-coupled receptors—are likely to have been present in the common ancestor of vertebrates and invertebrates [4]. Presumably as a result of convergent evolution based on these building blocks, connections between neurons display similar plasticity in vertebrates and invertebrates, including short-term, spike-timing-dependent and long-term plasticity [39,40]. Basic circuit architecture is similar in insects and vertebrates, for example lateral inhibition, feed-forward and feedback excitation and inhibition, and presynaptic inhibition [41,42].

The many cases of parallel evolution in the sensory and motor systems further illustrate the readiness with which features of nervous systems (and the genes that control them) can often respond to pertinent selective pressure based on exaptations (i.e. the reuse of previously evolved adaptations for an entirely different function over evolutionary time-scales). For example,

red sensitivity has evolved several times in insect colour vision [43], and in Lepidoptera this has repeatedly occurred by gene duplication of a ‘green’ sensitive opsin and subsequent spectral sensitivity shift to longer wavelengths by the same amino acid substitutions [44]. Numerous vertebrate lineages also show adaptive duplications or losses of visual pigment genes, as well as more subtle spectral tuning of their protein products via (sometimes parallel) amino acid substitutions [45–47]. In mammals, at least, the nervous systems appears well-preconfigured to instantly add a novel sensory dimension to its perception without evolutionary lag-time to adjust postreceptor neural circuitry [48], perhaps by means of general purpose decorrelation mechanisms [49]. Invertebrates seem no less flexible to respond adaptively to completely novel sensory-motor contingencies within a short period of time [50].

The parallel or convergent acquisition of neural circuits for performing different cognitive tasks is perhaps not surprising, because such changes could be brought about by a multitude of permutations of the existing molecular hardware [51]. In comparison, known examples of convergent evolution at the primary DNA sequence level are scarce, though this situation could soon change with the increasing rate at which new genomes are being sequenced. An instructive case is the parallel evolution of ultrasonic hearing in cetaceans and bats. The gene encoding the motor protein prestin (which confers high-frequency sensitivity in the outer hair cells in the cochlea) has undergone several identical amino acid replacements [20,21] as well as bursts of molecular adaptation in unrelated lineages of echolocating bats [52], and also between bats and toothed whales [20,21]. Subsequent discoveries of parallel sequence evolution in other genes expressed in the cochlear hair cells of bats and cetaceans suggest that the evolution of echolocation has involved convergent changes in multiple loci [53].

The potential for small genetic changes to have profound impacts on neuro-computational properties is perhaps best illustrated by studies of genetic mutation in humans and other taxa. For example, deleterious mutations in the human gene *FOXP2* are associated with deficits in language and speech development, probably caused by alterations to the cortical and sub-cortical neural circuitry [54,55], whereas the occurrence of just two adaptive amino acid replacements on the branch leading to humans since our split from chimpanzees has been implicated in the evolution of language itself [56]. How such drastic developmental and/or evolutionary effects could be brought about by evidently small genetic changes is better understood in the light of recent findings showing that the encoded transcription factor *FOXP2* regulates a range of downstream genes in neural tissue [57], and that the humanized protein targets particular regions in the brains of mice [58]. Results from *FoxP2* in non-humans, including observations of spatio-temporal expression patterns in the brains of song learning zebra finches [59] and impaired song imitation in this species following knockdown [60] suggest a more general role in vocal learning (reviewed by Bolhuis *et al.* [61]). Accelerated rates of

FoxP2 sequence evolution [62] coupled with parallel expression in auditory nuclei [63] have also been observed in divergent lineages of another group of vocal learners—the echolocating bats—though it is unclear whether these data relate to echolocation rather than learning *per se*.

On the other hand, and further demonstrating the tremendous potential of nervous systems to rewire themselves over evolutionary time, there are impressive examples of homologous neurons or circuits used in divergent functions, e.g. in some sand crabs where motor neurons became sensory stretch receptors [64]. In conclusion, the understanding of the evolution of behavioural–cognitive traits is greatly facilitated by considering the underlying mechanisms. Often, relatively minor alterations in circuitry might be necessary to produce novel behavioural capacities [4,19,65].

4. NATURAL VARIATION OF COGNITION WITHIN SPECIES AND SELECTION EXPERIMENTS

In questioning how easily cognition might evolve under pertinent selective regimes, it is of course crucial to explore the heritable variation for cognitive traits within species [66,67]. While many workers have treated individual variation in cognitive performance as noise, such variation is the raw material for evolution and therefore deserves close attention. In bees, for example, all aspects of learning behaviour and cognition are individually variable, and often relate to colony membership, suggesting genetic underpinnings [68–71]. Learning ability is highly relevant to biological fitness under natural conditions [72], and selection experiments on bees [73] and other insects [74] reveal that learning speed responds exceptionally well to selection. Interestingly, in work on the colour vision system of guppies, it has been experimentally shown that populations of the same species might respond to the same selective pressure by adjusting different mechanisms to mediate the same (or similar) behavioural abilities [75].

So far, selection experiments have often focused on associative learning, not the more advanced cognitive feats [37], perhaps because these are much less easy to test for large numbers of individuals. There is nonetheless little doubt that more advanced cognitive faculties also display individual variation in many if not most animal species; Darwin, for example, described individual variation of attention in monkeys [76]. In humans, the study of the genetic basis of individual variation in cognitive capacity is a rapidly expanding field [77], and indeed twin, family and adoption studies reveal that all human cognitive abilities have heritable components [78]. For individual differences in working memory, episodic memory, novelty seeking and reward processing, there is now information on some of the molecular–genetic underpinnings, and unsurprisingly such variation often involves multiple genes [77]. More data on non-human animals and traits naturally under selection are needed, but the overall message from this section is that because individual, heritable variations in cognitive traits are presumably widespread, it is predicted that populations should often respond rapidly to selective

pressure for certain cognitive feats. The absence of a given cognitive ability in an animal might not necessarily indicate constraints of the evolvability of the neural hardware, but instead the absence of a relevant selection pressure. There is also a caveat here: the general premise to infer homology from the observation that related species share the same cognitive traits (e.g. humans and chimpanzees) is of course based on the idea that cognitive traits are as ‘difficult’ to evolve as morphological ones. Humans and chimpanzees, for example, have evolved separately for many tens of thousands of generations, i.e. extensive time to evolve behavioural capacities by parallel or convergent evolution based on shared selective pressures, given that selection experiments for behavioural traits can often produce dramatic results within a dozen or so generations (although of course selection experiments so far have not produced true qualitative shifts in cognitive capacity).

5. WHAT IS COGNITIVE COMPLEXITY AND HOW DOES IT EVOLVE?

In asking how complex, or ‘advanced’ various forms of cognition are, and to compare them between animal species, there is often a tendency to rank various types of plasticity from simple (e.g. habituation, sensitization) through intermediate (from classical conditioning to rule learning) to advanced (human-like, e.g. theory of mind, metacognition, consciousness). The implication is often that the more ‘advanced’ forms are more difficult to evolve, and might require large brains. However, we have to ask by what criteria we might assess ‘complexity’—what exactly makes one form of cognition more advanced than another? A common assumption of cognitive scientists and behavioural biologists is that perception involves the ordering of sensory information into internal representations, and that cognition involves the manipulation of representations (derived from both perception and memory). If this is so, then defining cognitive complexity could, in principle, be quite straightforward. Organisms construct internal (cognitive) models of the world and cognitive complexity is just the complexity of these models. If we further assume that such models are computational, then cognitive complexity is quantifiable, because there are mathematical ways of describing complexity. The problem with this abstraction is that in no case do we yet have a complete computational simulation of an organism’s model of the world (i.e. of a real brain). However, even if we did, another question would then arise: if such cognitive models of the world vary in complexity, could they also vary in efficiency? Could a less complex model do the job just as well, or better [79]?

For example, would an internal spatial representation (cognitive map) of an animal’s environment represent greater complexity than a system for guiding navigational behaviour based on path integration [80]? One possibility to quantify the complexity of a cognitive feat might be to use the minimal cognition approach. It has recently been shown, for example, that behaviour commonly interpreted in terms of map-like guidance can be generated by a very simple

simulation containing no such explicit internal representation [81]. What are the minimal components needed to perform a given function? Given the absence of a complete simulation (a model of the brain's model), many computational studies have opted for the 'minimal cognition' approach. For example, dynamical systems studies combined with artificial evolution of algorithms for control of real or simulated agents (evolutionary robotics or evolutionary computation, respectively) suggest that the number of neurons required to simulate a minimal cognitive feat is exceedingly small. Continuous-time recurrent neural networks can be artificially evolved to undertake perceptual categorization of falling 'triangles' and 'squares' using active vision with only eight neurons [82]. Relational categorization of concepts such as *larger* or *smaller* can be achieved using five neurons [83]. By using models of synaptic plasticity and neuromodulation [84], and again using *in silico* artificial evolution to find efficient circuits, it was possible to discover eight neuron reinforcement learning circuits that can learn the quality of reward associated with a resource and exhibit probability matching and risk-aversion phenomena predicted by optimal foraging theory [85]. Further work has examined predator-prey coevolution using similarly small neural networks to control behaviour, and even examined small neural circuits for altruism and cooperation [86]. While the tasks solved by these networks are undoubtedly simplifications of those encountered by real animals in nature, the overall message is that seemingly 'advanced' cognitive capacities can often be mediated by relatively simple circuits.

Evolutionary modelling is useful for mathematically formalizing thought experiments to identify simple solutions capable of explaining complex behaviours for which one might have otherwise thought that more complex representations were required. Using *in silico* evolution, we can produce small circuit designs that could not have been easily generated by human design principles, demonstrating that evolution could have had access to the variation required to solve apparently complex cognitive problems using compact 'tricks'. Conclusions about the evolvability of real cognition are still tentative, however, because such simple model solutions are found within a relatively constrained search space, where the network parameters specified in the 'genome' scale in a polynomial fashion with network size (unlike real genomes). Moreover, the search space of real cognitive evolution is constrained by the structure of reality (i.e. previous adaptations) unlike in most *in silico* experiments, where the solutions are generally independent of the prior evolution of other adaptations.

Finally, we might note that the minimal cognition approach does not readily provide any principled way of quantifying cognitive complexity; the real problem may lie in understanding the hierarchical structure of animals' cognitive models of the world [87], which, in principle, is excluded from studies of minimal cognition. Nevertheless, an important conclusion is that the minimum number of neurons necessary to perform a variety of cognitive tasks is typically very small. Ultimately, this may allow us to itemize cognitive

'toolkits' of functions [22], whereby the more versatile the toolkit the greater the cognitive complexity.

6. DATA-DRIVEN APPROACHES TO BEHAVIOUR AND COGNITION

A recent development is to turn away from the widespread expectation-driven (top-down, deductive) approach to the analysis of behaviour and cognition, and to classify behaviour by automated procedures so they can be objectively measured and compared using what Branson *et al.* [88] have called an 'ethomics' approach. New technologies in motion capture and video analyses make an entirely hypotheses-free approach to the analysis of behaviour feasible [88–90].

For the future, it will be necessary to develop large-scale automated analytical tools to effectively mine the data collected with the aim of finding prototypical and atypical behaviours. To discover prototypical activity models, a useful approach is to implement procedures for clustering accumulated trajectory data into representative patterns [90]. We will ultimately have to break down behavioural sequences into their smallest identifiable units, and quantify them in terms of trajectories of body parts, their speed, distance, acceleration, deceleration, etc., thereby identifying behavioural prototypes [90–92] that can subsequently be strung together into various sequences to reconstruct meaningful natural behaviour. To encode the variability of the behavioural repertoires, it will be necessary to develop a dedicated alphabet and syntax of movements that can be effectively compared between individuals and species. An automated 'data mining' approach will also facilitate the discovery of new behaviour patterns that have so far escaped the attention of human observers. In this bottom-up approach, we are less constrained by one particular concept, but we are also much freer to observe the peculiarities of the animals' behaviours. Animal cognition and behaviour, in all their diversity, are unlikely to be wholly describable by the concepts that are derived from just one, very unusual species, *Homo sapiens*. By looking at many more animal species, under more test conditions, and by testing many, and smaller, i.e. more basic criteria (cognitive or behavioural units), we probably could build cognitive constructs that are more independent from the human world and therefore, ultimately, more informative [2].

It is clear that such an approach cannot stand on its own, and needs to be coupled with experimental manipulation, which in turn needs to be hypothesis-driven. Learnt behaviours can be tested in meaningful ways only by exposing animals to controlled stimuli, and these cannot be generated in a hypothesis-free manner. Additionally, learning may generate a practically infinite number of behavioural routines that might be difficult to pick up in clustering algorithms—consider, for example, that the diversity of flower handling procedures required of a generalist pollinator to extract nectar or pollen is presumably as great as the number of floral morphologies [93]. Nonetheless, these might consist of small-scale hard-wired motor routines strung together in flexible ways [94]. Again, we would reveal this only by breaking

down behaviour into small components, using methods as described earlier.

While the fully automated, bias-free analysis of behaviour is now becoming increasingly feasible, this is less straightforward with cognitive processes that might or might not have observable outcomes. There is no question that hypothesis-driven behavioural experiments are a necessary ingredient of studying animal cognition (although the hypotheses might more suitably be driven by the motivation for scientific enquiry rather than for confirming that animals are clever). Nonetheless, there is plenty of room for more bias-free approaches in the study of cognitive approaches as well.

For example, multi-electrode recordings provided profound insights into how the brain stores and organizes memories in the rodent hippocampus [95,96], and the number of cells recorded from simultaneously (more than 100 in some cases) is impressive and contributed substantially to the understanding of the neural ensemble code of the mammalian hippocampus. Although the settings in which the data are recorded are of course hypothesis-based, their subsequent analysis is largely data-driven, in that information contained about individual neuronal firing patterns, and their propagation and integration, needs to be extracted from the raw data by data mining processes. A recent neuroanatomical study, for example, succeeded in identifying and mapping 16 per cent of the approximately 100 000 neurons of the *Drosophila* brain [97], illustrating just how far we have progressed in the direction of understanding the circuitry of insects' brains. Other recent developments make the imaging of entire neural circuits, and possibly whole brains at micrometre resolution, increasingly feasible [98,99]. It is quite conceivable that as such technologies develop we will discover neural-computational solutions to cognitive tasks in non-human animals quite unlike those in humans (even where the behavioural outcomes might be similar). We propose that such bottom-up approaches reduce the importance of introspection for the 'verification' of cognitive constructs; they could therefore contribute to create a more objective, more independent, and less arbitrary methodology for comparative cognition.

Neural network modelling can provide useful pointers for neuroscientists to concentrate their efforts on what to explore, and here, too, a more open-ended approach is needed. Often, modellers search for a single computational solution that best explains an empirically determined phenomenon. An alternative approach would be an emphasis on diversity—for example, for a given cognitive problem, how many neural solutions might be generated, and how does this depend on the number of available neurons (and their connections)? Circuit functionality can be assessed by varying all parameters in discrete steps and keeping a complete record of simulation results, including the output for each varied parameter value under all combinations of parameter settings, as has been done in simulations to derive optimal colour coding systems where thousands of possible solutions were fully analysed [100]. A good example of a bottom-up approach in computational neuroscience

is a model of the fly mushroom body, which, rather than being built to mimic known behavioural affordances, instead implemented all neurobiological information available into a comprehensive circuitry model to subsequently ask which forms of learning might be produced by such circuitry [101]. The remarkable result was that, while the model predicted several known forms of elemental and non-elemental learning in *Drosophila*, it also predicted some forms of learning that had not yet been behaviourally confirmed [101]. This sort of modelling might indeed reveal previously undescribed forms of information processing that could subsequently be tested by behavioural experiments.

Finally, bottom-up approaches for comparing cognitive abilities among individuals, populations or taxa must consider the sequences of the underlying candidate genes, as well as their protein products, expression patterns and molecular targets. The very recent development of new sequencing technologies has revolutionized the rate at which new genome data are being generated and analysed [102], so allowing increasing numbers of taxa to be studied at depths previously possible for just a tiny number of model organisms. The associated boom in studies of phylogenomics, population genomics and genome-wide associations all present unprecedented opportunities for gene discovery, allowing us to distinguish between ancestral and derived character states for thousands of loci [103,104]. Combining such gene sequence data with transgenic and recombinant technologies—which are already being applied to studies of cognition [58,105]—offers a promising and powerful means of dissecting the commonalities and differences in neuro-computational and cognitive processing in a comparative framework.

7. SUMMARY

There is an urgent need to understand animal 'intelligence' not just by apparent levels of task complexity and the extent to which human observers are impressed by animal cleverness, but in neural-computational terms: how many neurons, with what connections, and what computational operations are necessary to solve a given task? Without such information, the principal challenge of comparative cognition will remain difficult to overcome: there is limited information in mapping behavioural phenomena onto a phylogeny to infer homology or convergence, so long as the underpinning mechanisms are unknown. The quest for understanding the precise neuron-to-neuron connectivity underlying cognitive processes can be addressed both from an empirical angle, as well as from a modelling perspective. To understand how (and how easily) cognition and behaviour evolve, we must understand the neural circuitry that mediates a given cognitive trait and the genes (and their regulation) involved in its expression.

REFERENCES

- 1 Maclean, E. L. *et al.* 2012 How does cognition evolve? Phylogenetic comparative psychology. *Anim. Cogn.* **15**, 223–238. (doi:10.1007/s10071-10011-10448-10078)

- 2 Döring, T. F. & Chittka, L. 2011 How human are insects, and does it matter? *Formosan Entomol.* **31**, 85–99.
- 3 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)
- 4 Chittka, L. & Niven, J. 2009 Are bigger brains better? *Curr. Biol.* **19**, R995–R1008. (doi:10.1016/j.cub.2009.08.023)
- 5 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)
- 6 Willems, R. M. 2011 Re-appreciating the *why* of cognition: 35 years after Marr and Poggio. *Front. Psychol.* **2**, 244. (doi:10.3389/fpsyg.2011.00244)
- 7 de Waal, F. B. M. & Ferrari, P. F. 2010 Towards a bottom-up perspective on animal and human cognition. *Trends Cogn. Sci.* **14**, 201–207. (doi:10.1016/j.tics.2010.03.003)
- 8 Chittka, L. & Skorupski, P. 2011 Information processing in miniature brains. *Proc. R. Soc. B* **278**, 885–888. (doi:10.1098/rspb.2010.2699)
- 9 Bolhuis, J. J. & Wynne, C. D. L. 2009 Can evolution explain how minds work? *Nature* **458**, 832–833. (doi:10.1038/458832a)
- 10 Frisch, K. v. 1967 *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.
- 11 Pearce, J. M. 2008 *Animal learning and cognition*, 3rd edn. New York, NY: Psychology Press.
- 12 Arnold, S. E. J., Savolainen, V. & Chittka, L. 2009 Flower colours along an alpine altitude gradient, seen through the eyes of fly and bee pollinators. *Arthropod-Plant Interactions* **3**, 27–43. (doi:10.1007/s11829-009-9056-9)
- 13 Chittka, L. & Menzel, R. 1992 The evolutionary adaptation of flower colors and the insect pollinators' color vision systems. *J. Comp. Physiol. A* **171**, 171–181.
- 14 Roth, G. & Dicke, U. 2005 Evolution of the brain and intelligence. *Trends Cogn. Sci.* **9**, 250–257. (doi:10.1016/j.tics.2005.03.005)
- 15 Bitterman, M. E. 1975 The comparative analysis of learning. *Science* **188**, 699–709. (doi:10.1126/science.188.4189.699)
- 16 Shettleworth, S. J. 2010 *Cognition, evolution and behavior*. Oxford, UK: Oxford University Press.
- 17 Seed, A., 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)
- 18 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)
- 19 Katz, P. S. 2011 Neural mechanisms underlying the evolvability of behaviour. *Phil. Trans. R. Soc. B* **366**, 2086–2099. (doi:10.1098/rstb.2010.0336)
- 20 Liu, Y., Rossiter, S. J., Han, X. Q., Cotton, J. A. & Zhang, S. Y. 2010 Cetaceans on a molecular fast track to ultrasonic hearing. *Curr. Biol.* **20**, 1834–1839. (doi:10.1016/j.cub.2010.09.008)
- 21 Liu, Y., Cotton, J. A., Shen, B., Han, X. Q., Rossiter, S. J. & Zhang, S. Y. 2010 Convergent sequence evolution between echolocating bats and dolphins. *Curr. Biol.* **20**, R53–R54. (doi:10.1016/j.cub.2009.11.058)
- 22 Emery, N. J. & Clayton, N. S. 2004 The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907. (doi:10.1126/science.1098410)
- 23 Kawasaki, M. 2009 Evolution of time-coding systems in weakly electric fishes. *Zool. Sci.* **26**, 587–599. (doi:10.2108/zsj.26.587)
- 24 Healy, S. D. & Rowe, C. 2007 A critique of comparative studies of brain size. *Proc. R. Soc. B* **274**, 453–464. (doi:10.1098/rspb.2006.3748)
- 25 Striedter, G. 2005 *Principles of brain evolution*. Sunderland, MA: Sinauer.
- 26 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)
- 27 Padberg, J., Franca, J. G., Cooke, D. F., Soares, J. G. M., Rosa, M. G. P., Fiorani, M., Gattass, R. & Krubitzer, L. 2007 Parallel evolution of cortical areas involved in skilled hand use. *J. Neurosci.* **27**, 10 106–10 115. (doi:10.1523/jneurosci.2632-07.2007)
- 28 Lazure, L. & Fenton, M. B. 2011 High duty cycle echolocation and prey detection by bats. *J. Exp. Biol.* **214**, 1131–1137. (doi:10.1242/jeb.048967)
- 29 Schnitzler, H.-U. & Denzinger, A. 2011 Auditory fovea and Doppler shift compensation: adaptations for flutter detection in echolocating bats using CF-FM signals. *J. Comp. Physiol.* **197**, 541–559. (doi:10.1007/s00359-010-0569-6)
- 30 Sheehan, M. J. & Tibbetts, E. A. 2008 Robust long-term social memories in a paper wasp. *Curr. Biol.* **18**, R851–R852. (doi:10.1016/j.cub.2008.07.032)
- 31 Gronenberg, W., Ash, L. E. & Tibbetts, E. A. 2008 Correlation between facial pattern recognition and brain composition in paper wasps. *Brain Behav. Evol.* **71**, 1–14. (doi:10.1159/000108607)
- 32 Brockmann, A. & Robinson, G. E. 2007 Central projections of sensory systems involved in honey bee dance language communication. *Brain Behav. Evol.* **70**, 125–136. (doi:10.1159/000102974)
- 33 Holloway, R. L. 2002 Brief communication: how much larger is the relative volume of area 10 of the prefrontal cortex in humans? *Am. J. Phys. Anthropol.* **118**, 399–401. (doi:10.1002/ajpa.10090)
- 34 Petrides, M., Cadoret, G. V. & Mackey, S. 2005 Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature* **435**, 1235–1238. (doi:10.1038/nature03628)
- 35 Spocter, M. A., Hopkins, W. D., Garrison, A. R., Bauernfeind, A. L., Stimpson, C. D., Hof, P. R. & Sherwood, C. C. 2010 Wernicke's area homologue in chimpanzees (*Pan troglodytes*) and its relation to the appearance of modern human language. *Proc. R. Soc. B* **277**, 2165–2174. (doi:10.1098/rspb.2010.0011)
- 36 Gallistel, C. R. & King, A. P. 2009 *Memory and the computational brain: why cognitive science will transform neuroscience*. Oxford, UK: Wiley-Blackwell.
- 37 Menzel, R. & Giurfa, M. 2001 Cognitive architecture of a mini-brain: the honeybee. *Trends Cogn. Sci.* **5**, 62–71. (doi:10.1016/S1364-6613(00)01601-6)
- 38 Webb, B. 2012 Cognition in insects. *Phil. Trans. R. Soc. B* **367**, 2715–2722. (doi:10.1098/rstb.2012.0218)
- 39 Niven, J. E. & Burrows, M. 2003 Spike width reduction modifies the dynamics of short-term depression at a central synapse in the locust. *J. Neurosci.* **23**, 7461–7469.
- 40 Cassenaer, S. & Laurent, G. 2007 Hebbian STDP in mushroom bodies facilitates the synchronous flow of olfactory information in locusts. *Nature* **448**, 709–712. (doi:10.1038/nature05973)
- 41 Burrows, M. & Laurent, G. 1993 Synaptic potentials in the central terminals of locust proprioceptive afferents generated by other afferents from the same sense organ. *J. Neurosci.* **13**, 808–819.
- 42 Burrows, M. 1996 *The neurobiology of an insect brain*. Oxford, UK: Oxford University Press.
- 43 Chittka, L. 1996 Does bee colour vision predate the evolution of flower colour? *Naturwissenschaften* **83**, 136–138. (doi:10.1007/BF01142181)

- 44 Frentiu, F. D., Bernard, G. D., Sison-Mangus, M. P., Brower, A. V. Z. & Briscoe, A. D. 2007 Gene duplication is an evolutionary mechanism for expanding spectral diversity in the long-wavelength photopigments of butterflies. *Mol. Biol. Evol.* **24**, 2016–2028. (doi:10.1093/molbev/msm132)
- 45 Yokoyama, S. & Yokoyama, R. 1996 Adaptive evolution of photoreceptors and visual pigments in vertebrates. *Annu. Rev. Ecol. Syst.* **27**, 543–567. (doi:10.1146/annurev.ecolsys.27.1.543)
- 46 Hunt, D. M., Carvalho, L. S., Cowing, J. A. & Davies, W. L. 2009 Evolution and spectral tuning of visual pigments in birds and mammals. *Phil. Trans. R. Soc.* **364**, 2941–2955. (doi:10.1098/rstb.2009.0044)
- 47 Zhao, H., Rossiter, S. J., Teeling, E. C., Li, C., Cotton, J. A. & Zhang, S. 2009 The evolution of color vision in nocturnal mammals. *Proc. Natl Acad. Sci. USA* **106**, 8980–8985. (doi:10.1073/pnas.0813201106)
- 48 Jacobs, G. H., Williams, G. A., Cahill, H. & Nathans, J. 2007 Emergence of novel color vision in mice engineered to express a human cone photopigment. *Science* **315**, 1723–1725. (doi:10.1126/science.1138838)
- 49 Skorupski, P. & Chittka, L. 2011 Is colour cognitive? *Optics Laser Technol.* **43**, 251–260. (doi:10.1016/j.optlastec.2008.12.015)
- 50 Wolf, R., Voss, A., Hein, S. & Heisenberg, M. 1992 Can a fly ride a bicycle? *Phil. Trans. R. Soc. Lond. B* **337**, 261–269. (doi:10.1098/rstb.1992.0104)
- 51 Shou, C., Bhardwaj, N., Lam, H. Y. K., Yan, K.-K., Kim, P. M., Snyder, M. & Gerstein, M. B. 2011 Measuring the evolutionary rewiring of biological networks. *PLoS Comput. Biol.* **7**, e1001050. (doi:10.1371/journal.pcbi.1001050)
- 52 Li, G., Wang, J., Rossiter, S. J., Jones, G., Cottont, J. A. & Zhang, S. 2008 The hearing gene *Prestin* reunites echolocating bats. *Proc. Natl Acad. Sci. USA* **105**, 13 959–13 964. (doi:10.1073/pnas.0802097105)
- 53 Davies, K., Cotton, J., Kirwan, J., Teeling, E. & Rossiter, S. J. 2011 Parallel signatures of sequence evolution among hearing genes in echolocating mammals: an emerging model of genetic convergence. *Heredity* **108**, 480–489. (doi:10.1038/hdy.2011.119)
- 54 Fisher, S. E. & Scharff, C. 2009 *FOXP2* as a molecular window into speech and language. *Trends Genet.* **25**, 166–177. (doi:10.1016/j.tig.2009.03.002)
- 55 Enard, W. 2011 *FOXP2* and the role of cortico-basal ganglia circuits in speech and language evolution. *Curr. Opin. Neurobiol.* **21**, 415–424. (doi:10.1016/j.conb.2011.04.008)
- 56 Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., Monaco, A. P. & Paabo, S. 2002 Molecular evolution of *FOXP2*, a gene involved in speech and language. *Nature* **418**, 869–872. (doi:10.1038/nature01025)
- 57 Vernes, S. C., Spiteri, E., Nicod, J., Groszerm, M., Taylor, J. M., Davies, K. E., Geschwind, D. H. & Fisher, S. E. 2007 High-throughput analysis of promoter occupancy reveals direct neural targets of *FOXP2*, a gene mutated in speech and language disorders. *Am. J. Hum. Genet.* **81**, 1232–1250. (doi:10.1086/522238)
- 58 Reimers-Kipping, S., Hevers, W., Paeaebo, S. & Enard, W. 2011 Humanized *Foxp2* specifically affects cortico-basal ganglia circuits. *Neuroscience* **175**, 75–84. (doi:10.1016/j.neuroscience.2010.11.042)
- 59 Haesler, S., Wada, K., Nshdejan, A., Morrissy, E. E., Lints, T., Jarvis, E. D. & Scharff, C. 2004 *FoxP2* expression in avian vocal learners and non-learners. *J. Neurosci.* **24**, 3164–3175. (doi:10.1523/jneurosci.4369-03.2004)
- 60 Haesler, S., Rochefort, C., Georgi, B., Licznarski, P., Osten, P. & Scharff, C. 2007 Incomplete and inaccurate vocal imitation after knockdown of *FoxP2* in songbird basal ganglia nucleus area X. *PLoS Biol.* **5**, e321. (doi:10.1371/journal.pbio.0050321)
- 61 Bolhuis, J. J., Okanoya, K. & Scharff, C. 2010 Twitter evolution: converging mechanisms in birdsong and human speech. *Nat. Rev. Neurosci.* **11**, 747–759. (doi:10.1038/nrn2931)
- 62 Li, G., Wang, J., Rossiter, S. J., Jones, G. & Zhang, S. 2007 Accelerated *FoxP2* evolution in echolocating bats. *PLoS ONE* **2**, e900. (doi:10.1371/journal.pone.0000900)
- 63 Metzner, W. & Schuller, G. 2010 Vocal control in echolocating bats. In *Handbook of mammalian vocalizations* (ed. S. Brudzynski), pp. 403–415. Amsterdam, The Netherlands: Elsevier.
- 64 Paul, D. H. 2007 Evolutionary neuroethology: a case study: origin and evolution of novel forms of locomotion in Hippid sand crabs. In *Evolution of nervous systems* (ed. J. H. Kaas), pp. 99–119. Oxford, UK: Academic Press.
- 65 Ocker, W. & Hedwig, B. 1996 Interneurons involved in stridulatory pattern generation in the grasshopper *Chorthippus mollis* (Charp.). *J. Exp. Biol.* **199**, 653–662.
- 66 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)
- 67 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)
- 68 Chittka, L. & Thomson, J. D. 1997 Sensori-motor learning and its relevance for task specialization in bumble bees. *Behav. Ecol. Sociobiol.* **41**, 385–398. (doi:10.1007/s002650050400)
- 69 Chittka, L. & Reinhold, H. 1999 Towards an individual-based approach to insect learning. In *Proc. 27th Göttingen Neurobiology Conf.* (eds N. Elsner & U. Eysel), p. 257. Berlin, Germany: Thieme.
- 70 Raine, N. E., Ings, T. C., Dornhaus, A., Saleh, N. & Chittka, L. 2006 Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Ad. Study Behav.* **36**, 305–354. (doi:10.1016/S0065-3454(06)36007-X)
- 71 Page, R. E. J., Schneir, R., Erber, J. & Amdam, G. V. 2006 The development and evolution of division of labor and foraging specialization in a social insect (*Apis mellifera* L.). *Curr. Top. Dev. Biol.* **74**, 253–286. (doi:10.1016/S0070-2153(06)74008-X)
- 72 Raine, N. E. & Chittka, L. 2008 The correlation of learning speed and natural foraging success in bumble-bees. *Proc. R. Soc. B* **275**, 803–808. (doi:10.1098/rspb.2007.1652)
- 73 Brandes, C. 1987 Effects of bidirectional selection on learning behavior in honeybees (*Apis mellifera capensis*). In *Chemistry and biology of social insects* (eds J. Eder & H. Rembold), pp. 192–193. Muenchen, Germany: J. Peperny.
- 74 Lofdahl, K. L., Holliday, M. & Hirsch, J. 1992 Selection for conditionability in *Drosophila melanogaster*. *J. Comp. Psychol.* **106**, 172–183. (doi:10.1037/0735-7036.106.2.172)
- 75 Endler, J. A., Basolo, A., Glowacki, S. & Zerr, J. 2001 Variation in response to artificial selection for light sensitivity in guppies (*Poecilia reticulata*). *Am. Nat.* **158**, 36–48. (doi:10.1086/320862)
- 76 Darwin, C. 1871 *The descent of man, and selection in relation to sex*. London, UK: John Murray.

- 77 Robbins, T. W. & Kousta, S. 2011 Uncovering the genetic underpinnings of cognition. *Trends Cogn. Sci.* **15**, 375–377. (doi:10.1016/j.tics.2011.07.006)
- 78 Bouchard, T. J. & McGue, M. 2003 Genetic and environmental influences on human psychological differences. *J. Neurobiol.* **54**, 4–45. (doi:10.1002/neu.10160)
- 79 Chater, N. 1999 The search for simplicity: a fundamental cognitive principle? *Q. J. Exp. Psychol. A* **52**, 273–302. (doi:10.1080/027249899391070)
- 80 Chittka, L., Kunze, J., Shipman, C. & Buchmann, S. L. 1995 The significance of landmarks for path integration of homing honey bee foragers. *Naturwiss* **82**, 341–343. (doi:10.1007/BF01131533)
- 81 Cruse, H. & Wehner, R. 2011 No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comput. Biol.* **7**, e1002009. EP.
- 82 Beer, R. D. 2003 The dynamics of active categorical perception in an evolved model agent (with commentary and response). *Adapt. Behav.* **11**, 209–243. (doi:10.1177/1059712303114001)
- 83 Williams, P. L., Beer, R. D. & Gasser, M. 2008 An embodied dynamical approach to relational categorization. In *Proc. 30th Annual Conf. Cognitive Science Society, Washington DC, 23–28 July 2008* (eds B. C. Love, K. McRae & V. M. Sloutsky), pp. 223–228.
- 84 Soltoggio, A., Dürr, P., Mattiussi, C. & Floreano, D. 2007 Evolving neuromodulatory topologies for reinforcement learning-like problems. In *Proc. 2007 IEEE Congress on Evolutionary Computation, Singapore, 25–28 September 2007*, pp. 2471–2478. (doi:10.1109/CEC.2007.4424781)
- 85 Niv, Y., Joel, D., Meilijson, I. & Ruppig, E. 2002 Evolution of reinforcement learning in uncertain environments: a simple explanation for complex foraging behaviors. *Adapt. Behav.* **10**, 5–23. (doi:10.1177/10597123020101001)
- 86 Floreano, D. & Keller, L. 2010 Evolution of adaptive behaviour in robots by means of darwinian selection. *PLoS Biol.* **8**, e1000292. (doi:10.1371/journal.pbio.1000292)
- 87 Dayan, P. & Niv, Y. 2008 Reinforcement learning: the good, the bad and the ugly. *Curr. Opin. Neurobiol.* **18**, 185–196. (doi:10.1016/j.conb.2008.08.003)
- 88 Branson, K., Robie, A. A., Bender, J., Perona, P. & Dickinson, M. H. 2009 High-throughput ethomics in large groups of *Drosophila*. *Nat. Methods* **6**, U451–U477. (doi:10.1038/nmeth.1328)
- 89 Benjamini, Y., Fonio, E., Galili, T., Havkin, G. Z. & Golani, I. 2011 Quantifying the buildup in extent and complexity of free exploration in mice. *Proc. Natl Acad. Sci.* **108**(Suppl. 3) 15 580–15 587. (doi:10.1073/pnas.1014837108)
- 90 Braun, E., Geurten, B. & Egelhaaf, M. 2010 Identifying prototypical components in behaviour using clustering algorithms. *PLoS ONE* **5**, e9361. (doi:10.1371/journal.pone.0009361)
- 91 Maggio, E. & Cavallaro, A. 2011 *Video tracking: theory and practice*. Chichester, UK: John Wiley & Sons.
- 92 Anjum, N. & Cavallaro, A. 2008 Multi-feature object trajectory clustering for video analysis. *IEEE Trans. Circuits Syst. Video Technol.* **18**, 1555–1564. (doi:10.1109/TCSVT.2008.2005603)
- 93 Chittka, L. 1998 Sensorimotor learning in bumblebees: long term retention and reversal training. *J. Exp. Biol.* **201**, 515–524.
- 94 Gould, J. L. & Marler, P. 1984 Ethology and the natural history of learning. In *The biology of learning* (eds P. Marler & H. S. Terrace), pp. 47–74. Berlin, Germany: Springer.
- 95 Wilson, M. A. & McNaughton, B. L. 1994 Reactivation of hippocampal ensemble memories during sleep. *Science* **265**, 676–679. (doi:10.1126/science.8036517)
- 96 McNaughton, B. L. et al. 1996 Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J. Exp. Biol.* **199**, 173–185.
- 97 Chiang, A.-S. et al. 2010 Three-dimensional reconstruction of brain-wide wiring networks in *Drosophila* at single-cell resolution. *Curr. Biol.* **21**, 1–11. (doi:10.1016/j.cub.2010.11.056)
- 98 Dodt, H. U. et al. 2007 Ultramicroscopy: three-dimensional visualization of neuronal networks in the whole mouse brain. *Nat. Methods* **4**, 331–336. (doi:10.1038/nmeth1036)
- 99 Jahrling, N., Becker, K., Schonbauer, C., Schnorrer, F. & Dodt, H. U. 2010 Three-dimensional reconstruction and segmentation of intact *Drosophila* by ultramicroscopy. *Front. Syst. Neurosci.* **4**, 1. (doi:10.3389/neuro.3306.3001.2010)
- 100 Chittka, L. 1996 Optimal sets of colour receptors and opponent processes for coding of natural objects in insect vision. *J. Theor. Biol.* **181**, 179–196. (doi:10.1006/jtbi.1996.0124)
- 101 Wessnitzer, J., Young, J. M., Armstrong, J. D. & Webb, B. 2012 A model of non-elemental olfactory learning in *Drosophila*. *J. Comput. Neurosci.* **32**, 197–212. (doi:10.1007/s10827-011-0348-6)
- 102 Metzker, M. L. 2010 Applications of next-generation sequencing technologies: the next generation. *Nat. Rev. Genet.* **11**, 31–46. (doi:10.1038/nrg2626)
- 103 Davis, O. S. P., Butcher, L. M., Docherty, S. J., Meaburn, E. L., Curtis, C. J. C., Simpson, M. A., Schalkwyk, L. C. & Plomin, R. 2010 A three-stage genome-wide association study of general cognitive ability: hunting the small effects. *Behav. Genet.* **40**, 759–767. (doi:10.1007/s10519-010-9350-4)
- 104 Kunstner, A. et al. 2010 Comparative genomics based on massive parallel transcriptome sequencing reveals patterns of substitution and selection across 10 bird species. *Mol. Ecol.* **19**, 266–276. (doi:10.1111/j.1365-294X.2009.04487.x)
- 105 Wood, N. I., Glynn, D. & Morton, A. J. 2011 ‘Brain training’ improves cognitive performance and survival in a transgenic mouse model of Huntington’s disease. *Neurobiol. Dis.* **42**, 427–437. (doi:10.1016/j.nbd.2011.02.005)