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Natural variation in learning and memory

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Learning is widespread in the animal kingdom. From the small nematode worm *Caenorhabditis elegans* to humans, learning appears to play a central role in adaptation to local spatial and temporal environmental conditions. Though the neurobiological mechanisms of learning and memory have been intensively studied, the function and adaptive significance of learning has only recently received interest. Using learning, animals may progressively adjust their behavior in response to new environmental conditions, suggesting benefits of learning on animal performance, at least in the short term. How does learning affect the overall fitness of an animal? What are the fitness benefits and costs of learning? How can we explain the natural variation in learning ability observed between individuals, between populations of the same species or between closely related species? What are the ecological circumstances that favor the evolution of learning? There are all emerging questions that are central to a better understanding of the evolution of cognition and animal adaptation. Here I review the recent evidence showing that learning and memory are molded by an animal's lifestyle within its ecological niche.

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Introduction

Perhaps first motivated by a desire to better understand human brain functioning, scientists have long been interested in describing and comparing cognitive abilities of animals, including humans. There have been some difficult challenges to overcome in order to develop cognitive task protocols. First, compared to other phenotypic traits, the measurement of cognitive performance is complicated by a lack of unique and standardized physical measurement tools. Cognitive ability can only be measured indirectly, by measuring the behavioral response of an animal facing a task. Second, an individual's performance depends not only on its cognitive ability but also on contextual variables, such as motivation to perform a specific task or a requirement for a specific response. These challenges have led to intense debate and controversy within the field of comparative cognition (reviewed in [1]). However, accumulated field and laboratory data, especially on vertebrates, showed that animal cognitive ability is greater than previously thought. These studies also revealed that not only are some common cognitive processes shared by all animals, but there is also strong interspecific or intraspecific variation in the way animals learn specific tasks and remember how to complete these tasks. The existence of natural variation in learning and memory moved the field of cognitive biology progressively toward incorporating the importance of natural selection through adaptation to the local environment into models of cognitive abilities. Development in the fields of neurobiology, genetics, computational biology, evolutionary biology, and behavioral ecology currently offers new tools and open new perspectives that provide a better understanding of the evolution of cognition and animal adaptation and also of the mechanisms that allow such adaptation.

Here I review the recent evidence for natural variation in learning and memory and discuss how this variation in learning and memory relates to variation in ecological or social adaptation.

Genetic variation in learning and memory

As with any other phenotypic trait, learning and memory can only evolve if there is genetic variation in these traits. Evidence of individual genetic variation in learning and memory continues to grow. Using an ecologically relevant learning protocol, Mery and Kawecki [2] artificially selected for improved learning and memory over several generations in *Drosophila melanogaster*. Within a few dozen generations, learning and memory of artificially selected flies were significantly better than that of the base population, which showed strong genetic variation for that trait. The genes underlying these experimentally induced evolutionary changes have not yet been identified. Several mutants with strong defects in learning and memory have been identified in *Drosophila* [3] and in *Caenorhabditis elegans* [4]. These mutants are invaluable tools for studies of how learning and memory are processed. However, these mutant alleles usually have other deleterious effects [5,6] and would presumably be strongly counter-selected in natural populations. Whether the natural genetic variation for learning and memory involves milder alleles of those loci or some other loci altogether [6] remains an open question. In humans, the recent development of high-throughput genotyping methods has made it possible to identify genes related to inter-individual variation in cognitive traits such as short-term memory [7••]. Unlike the candidate gene approach, these methods allow for genome-wide association studies of polygenetic phenotypes that can lead to the identification of novel genes. These powerful methods could open perspectives on the study of the natural evolutionary forces that maintain this polymorphism and other cognitive variation, which to date have only been studied in model organisms such as *Drosophila*. As an example, the well-characterized natural polymorphism in *Drosophila* that occurs at the foraging gene (*for*), which encodes a cGMP-dependent protein kinase (PKG), affects a range of phenotypic traits, including learning [8].

It is worth noting that the development of cognitive capacities is not only determined genetically, it also depends on a number of environmental and social factors [9] which can overwhelm and mask genetic variation. When mice with targeted mutations that compromise synaptic plasticity and learning are housed in an enriched environment, learning deficits due to the mutant background can be overcome [10].

How these natural genetic variations in learning ability, memory dynamics, and cognitive strategies are maintained has been studied intensively over the last few years [8,11–13]. Natural selection will favor a trait if there is genetic variation for that trait and if the trait improves lifetime reproductive success, that is, if the associated fitness benefits outweigh the fitness costs. The balance between benefits and costs depends on the ecological conditions experienced by individuals.

Variation in learning and memory as an adaptation to ecological conditions

One of the most commonly cited hypotheses for the evolution of learning is that it allows an individual to adapt to environmental changes. The most fundamental and universal mechanism for handling environmental variation relies on gene regulation [14]. In honeybee colonies, division of labor is highly sensitive to environmental changes. The behavioral switch from brood care to foraging depends on regulation of the *for* gene [15]. This is an adaptive response that develops over generations through the action of natural selection and that allows honeybees to deal with a highly predictable situation. Learning provides an additional level of plasticity in less predictable environments, allowing an individual to respond to situations that are unique to a specific time and space [16]. One would thus expect to find better learning ability in variable environments than in constant environment. Black-capped chickadee (*Poecile atricapillus*) populations that inhabit unstable environments learn more easily and are better able to remember the location of food caches than populations in more stable and favorable environments [17]. Another source of environmental variation arises when individuals move between environments, and are therefore likely to experience different ecological conditions. Species that can tolerate these changes should show good invasive capacities. The invasive green crab *Carcinus maenas* is better at learning how to find hidden food than is the native blue crab *Callinectes sapidus* in sympatric populations in the northeastern US [18].

Memory retention should also depend on environmental stability and predictability. Recently, the process of forgetting has come to be seen as an adaptive process in its own right, rather than simply a failure to remember [19]. The number of conditioning trials necessary to induce a long-term memory response has been found to be highly variable among generalist parasitoid species; for some of them, a single experience may directly induce behavioral modification while others never respond to multiple conditioning trials [20]. *Cotesia glomerata* and *Cotesia rubecula* are two closely related parasitoid species of white cabbage caterpillars. The species differ by their host preference and the distribution of these hosts; *C. glomerata*'s host lives in aggregated groups whereas *C. rubecula*'s host is solitary and is found on dispersed plants. Recent studies have found differences in learning and memory dynamics between the two species [21••]. *C. rubecula* required repeated rest periods between training sessions to modify its behavior and form stable long-term memory whereas *C. glomerata* formed long-term memory after a single training session. This interesting difference may be related to the difference in host distribution. For *C. rubecula*, the probability of finding a second host on the same plant may be low compared to *C. glomerata*; thus, it would be maladaptive for *C. rubecula* to store information about host location too rapidly.

These field and laboratory experiments suggest a link between environmental heterogeneity and predictability and learning and memory. As the probability of environmental change decreases, the benefits of learning should also decrease and an innate behavioral response adapted to the conditions of the common environment should evolve [22]. A recent study on butterfly host selection behavior recently challenged this view [23•]. The butterfly *Pieris rapae* shows an innate attraction to green — the most commonly encountered plant color. When facing an assemblage of green plants, female butterflies rapidly discriminated between host and non-host species. However, in an assemblage of red plants, females initially performed poorly but progressively learned the difference between host and non-host species. This study highlights the complex interaction between innate bias and learning ability. The commonness of green environments in nature may have driven the evolution of an innate bias toward green but the rare occurrence of red environments may have maintained learning.

It is notable that we still know very little about the actual impact of learning in natural conditions and how variation in learning ability reflects different behavioral strategies. In particular, we do not know how laboratory experiments, using assays that have no obvious relationship to an animal's ecology, can be extrapolated to natural conditions.

Constraints and limits to the actual comparative approach

When studying variation in learning and memory, more and more research, especially in vertebrates, use brain size as an 'easy', measurable proxy. Bigger brains are assumed to provide more behavioral flexibility at the cost of increased metabolic demand. Brain size is a much easier measure than complex and limited behavioral experiments and should reflect more general cognitive abilities that are not specific to a single learning task. This hypothesis, however, relies on two critical assumptions: that there is a relationship between learning ability and quantitative variation in neural structures [16,24,25] and that there is a relationship between quantitative variation in neural structures and metabolic costs. It is, however, difficult to precisely define and compare behavioral metrics and to compare interspecific brain regions [26]. Overall, brain size may not be a useful indicator of cognitive ability as brains are composed of many components that are not related to cognition. In recent years, studies on invertebrates, in particular, have challenged the idea of a relationship between brain size and learning ability [27•,28] and opened new perspectives on the evolution of cognition.

Invertebrate animals, which are usually very small, are potentially confronted with several constraints to the design of their neural structures. Following 'Haller's rule' [29] — which states that larger animal species have larger absolute brain size but smaller relative brain size than smaller species — invertebrates should pay disproportionately high metabolic costs to maintain their relatively large neural structures. In some species, the relative size of the brain is astonishing, such as in the small ant *Brachymyrmex* sp. ($\sim$0.04 mg) for which the brain represents 15% of the total body size [30]. For the same ratio (brain size/body mass), invertebrates sustain much smaller body mass than vertebrates and have managed to overcome constraints related to miniaturization. This raises questions whether it is appropriate to generalize conclusions about how the nervous system functions among taxa. Variation in axon diameter, neuronal morphology and the volume of sensory structure is known to affect information processing and energetic costs [31,32]. Comparisons among distant phylogenetic species are thus likely to be complicated by the fact that a similar volume of neural structures may consume different amounts of energy. Still, if the relative brain size of invertebrates correlates positively with basal metabolic rate, as found in vertebrates [33], small invertebrates should pay a disproportionate constitutive costs of brain maintenance. Additionally, as the computational power of a brain depends on its absolute size, small brains should require a higher density of metabolic activity to maintain similar neural performance to that of larger brains [32]. Reducing these costs could mean a reduction in the computational power and, consequently, a reduction in cognitive ability. Although it may be intuitively obvious, the relationship between cognitive ability and brain size is far from clear [27•,34]. It is difficult to objectively compare cognitive abilities, especially between species. Some authors used the repertoire of learning tasks an animal was capable of performing as an indicator of cognitive ability [27•,35–37]. Recently, however, work on learning and memory in invertebrates has shown that even very small invertebrates can solve a vast array of learning tasks that are comparable to those performed by vertebrates. *C. elegans* exhibits complex behavioral modalities such as habituation and sensitization [38,39], associative learning [40], and an ability to learn to associate its spatial location with the presence of food [41]. *D. melanogaster* shows aversive and appetitive associative learning [42,43], operant learning [44], spatial learning [45], social learning [46•], and non-elemental forms of learning [47]. Honeybee can even perform abstract discrimination [48]. In fact, the range of biological questions that can be answered by studying invertebrates is continually expanding, and new behavioral assays continue to reveal new limits of invertebrate cognition. A difficulty of using this qualitative comparative method concerns the fact that all tasks are considered as equally demanding of neural capabilities. Neural network simulations suggest that different learning tasks may involve different numbers of neurons and that these numbers are in fact extremely low [27•,49]. Using network architecture inspired by insects' mushroom bodies, associative learning [49] and non-elemental learning [50] could be simulated using extremely low set of parameters. Considering the strong selection pressure that should operate on insect brains to reduce superfluous costs, this may suggest that most invertebrates are not cognitively limited in terms of the repertoire of learning tasks they are capable of performing.

If, in invertebrates, there is no strong constraint on the breadth of the learning repertoire, improving learning performance for a specific task should be possible but may require additional neural tissue and consequently increase constitutive costs. In the simulation described above, increasing the number of Kenyon cells significantly improved non-elemental learning performance [50].

Conclusion

The general occurrence of learning in most animals studied so far raises questions about the relationship between ecological constraints and the evolution of learning. Learning appears to be much more widespread than previously thought and may not always fit with a simple 'Goldilocks principle', in which it is necessarily subject to specific limits. Laboratory and field studies have revealed that invertebrates rely heavily on learning and can use different forms of learning. The more we analyze learning in different species, the more initial cognitive differences between species seems to vanish, especially when considering the various forms of cognitive capacities recently discovered in insects. The capacity for learning might be a general property of all neural circuitry. As discussed by Papaj and Lewis [51], learned behavior may be an ancestral form. The evolution of learning cannot be restricted to an adaptation to environmental fluctuations; studies should integrate more ecological and social factors that may affect its evolution. The understanding of the maintenance and evolution of learning and memory in natural population is only at its beginning and would greatly benefit from an integration of evolutionary biology, neurobiology, behavioral ecology, genetics, and psychology to reach a general framework.

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