Review

Costs of memory: lessons from 'mini' brains

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Variation in learning and memory abilities among closely related species, or even among populations of the same species, has opened research into the relationship between cognition, ecological context and the fitness costs, and benefits of learning and memory. Such research programmes have long been dominated by vertebrate studies and by the assumption of a relationship between cognitive abilities, brain size and metabolic costs. Research on these 'large brained' organisms has provided important insights into the understanding of cognitive functions and their adaptive value. In the present review, we discuss some aspects of the fitness costs of learning and memory by focusing on 'mini-brain' studies. Research on learning and memory in insects has challenged some traditional positions and is pushing the boundaries of our understanding of the evolution of learning and memory.

Keywords: learning; memory; evolution; costs; insect

1. INTRODUCTION

The essence of learning as an adaptation is in how an animal modifies its behaviour with experience to better deal with the environment [1]. While it is traditionally and tacitly assumed that learning is beneficial, direct measurements of the benefits of learning and memory in terms of fitness have only very recently become a focus of research (e.g. [2–6]). That learning and memory may also have costs is recognized (e.g. [7,8]), but poorly quantified. Within the last decade, an increasing number of studies have experimentally addressed the balance between fitness costs and benefits using insects as biological models. Their relatively small brain, the ease of neurobiological and genetic manipulation, their extraordinary diversity in terms of lifestyle and habitat, and the possibility to access direct fitness measurements are some key factors that have made insects promising models for these studies. It is our intention to review the evidence, chiefly through the lens provided by studies on insects, regarding assumptions about the relationships between cognitive abilities, brain size and metabolic costs. We then consider the experimental support for costs of learning and memory, particularly, in terms of how studies on insects are helping to delineate the differences between induced versus constitutive costs, and processing versus storage costs.

The abilities to learn and remember vary between and within species. Heritability of learning ability has been demonstrated with the use of breeding designs (e.g. honeybees [9]; *Leptopilina* [10]) and selection experiments (honeybees [11]; *Drosophila* [12]; rats [13]; blow flies [14]), indicating that at least some natural populations harbour ample genetic variation for learning and memory. Brain morphology also varies within insects and other groups, as observed in brain structure volume, neuron morphology, neuron number and other traits (e.g. [15–19]). While there is an increasing documentation of natural within-species variation in learning rate and memory (e.g. [20–23]), there remain considerable and well-documented difficulties to delineating how species differ in their abilities [24]. One dominant position in comparative analyses has been to use proxies, such as brain size, corrected for body size, as a proxy for cognitive skills (e.g. [25–28]).

Comparative evidence does suggests that deviations in brain size from allometry tend to correlate with aspects of ecology and behaviour [29]. Studies on the relationship between sensory processing units, specifically, and ecology provide the strongest verification that natural selection acts on brain structures (e.g. [30,31]). With regard to a link between brain size and learning ability, perhaps the best evidence comes from the observed correlation between hippocampus size and spatial learning in mammals and food-storing birds ([32]; but see [33]). Although the evidence is less compelling at this point, the mushroom bodies of insects—which act as higher order processing units in insect brains—appear more structurally complex in species with more complex feeding behaviours [34,35]. As such, hypotheses have been developed around the costs of large and complex brains, especially regarding how the evolution of brain size affects life-history traits, such as time to maturity or length of developmental stages (e.g. [36,37]).

However, the conclusion that relative brain size has a causal effect on learning and memory abilities is problematic. Healy & Rowe [38] noted that problems with data quality and also with lack of evidence for causation, versus correlation, plague the literature. For instance, it is striking how correlations between ecology and brain size

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can be broken just by the addition of one more variable to a multiple regression model (see [39] and [40]). Additionally, brain size appears to be positively correlated with *quantitative* improvements in cognitive abilities (e.g. sensory acuity), rather than *qualitative* improvements (e.g. size of behavioural repertoires [41]). We shall also see the difficulties with linking metabolic costs to brain size across taxa. Precise evidence for metabolic costs has come from studies on insects, and we will discuss how insect brains may be the system best suited to make progress. In part because of the lesson that brain size is not so simply related to cognitive abilities, we do not yet have a good understanding of the costs of general cognitive skills, and even less so for specific cognitive skills.

2. RELATIONSHIP BETWEEN COGNITIVE ABILITIES, BRAIN SIZE AND METABOLIC COSTS

(a) *Link between cognitive abilities and brain size*
Careful examination of dozens of insect species has revealed large behavioural repertoires, a significant proportion of them including finely tuned motor responses, despite brains that usually contain only several hundred thousand neurons. These measures of behavioural complexity, while imperfect, indicate that insects can be as sophisticated as some mammals [41]. While the honeybee has become a classic example with more than 50 distinct behavioural patterns [41], other Hymenoptera, and even *Drosophila*, hold the ability to perform complex cognitive tasks [42–45]. Perhaps this should not be a surprise given that neural network studies have shown that the minimum number of neurons necessary to perform a variety of cognitive tasks are extremely small [46,47].

Aside from the complex behaviours they show, insects also demonstrate striking learning abilities, from the simplest forms of associative learning to more elaborate cognitive skills tasks including numerosity [48,49], categorization [50,51] and interval timing [52]. As expected for organisms displaying such cognitive abilities, insect brains have not only simple neural units that process specific information, but also central, higher order units—such as the mushroom bodies [53,54], among others—that allow them to integrate various types of information into adaptive behavioural outputs [55,56].

As stated previously, increased brain size is often correlated with quantitative improvements in cognitive function [41]. Larger brains usually show larger information-specific processing units, implying increased sensory resolution [31,57,58]. From an evolutionary point of view, such increased resolution would probably result in benefits (e.g. more precise recognition of food sources, mates and predators), given certain costs. However, a similar increase in neurons in a central unit would provide a better integration of already available information, opening new cognitive and behavioural possibilities [56]. There is also potentially a trade-off between allocation of energy and growth to information-specific neural units versus integrating units.

(b) *Link between brain size and metabolic costs*
Brains are costly organs in both vertebrates and invertebrates, as indicated by the large amounts of energy spent on their maintenance and functioning relative to basal metabolic rates [59]. From an evolutionary

perspective, this raises the question of how different organisms deal with the costs and benefits of learning abilities in relation to their habitats, life-history traits and other functions such as osmoregulation (i.e. the 'expensive tissue' hypothesis [60]). In this respect, recent breakthroughs from the study of insect brains have underlined the diversity of energetic costs associated with particular brain functions in related species. Niven *et al.* [61] estimated the energy expenditure and information rates of homologous photoreceptors in four Dipteran species. In photoreceptors, the prominent energy consumption stems from the activity of the $3Na^+/2K^+$ATPase, which actively maintains ion gradients across the membrane [59]. Consequently, energy consumption is high during rest periods as well as during information transmission [61,62]. Larger and more active fly species, *Calliphora vicina* and *Sarcophaga carnaria*, possess photoreceptors that are able to transmit many more bits of information per photon received (owing to higher signal-to-noise ratio and ample bandwidth) than the less active fly species, *Drosophila virilis* and *Drosophila melanogaster*. However, this improved performance incurred substantially higher energy costs, both at rest and while signalling (approx. 20-fold and 25-fold larger costs in large versus small flies in the dark and bright daylight). Thus, information processing in the larger flies was less energy efficient than in their smaller counterparts. This differential investment in a given sensory system, its performance and hence its metabolic cost, most probably reflects the species' ecological niche [63].

Although similar relationships can be envisaged for other peripheral sensory structures, the relationship between information processing, energy consumption and the size of higher centres remains unclear. The efficacy of energy-efficient coding schemes can change with size (e.g. graded versus action potentials and sparse coding), making direct comparisons difficult. Thus, direct quantification of the energetic costs, performance and size of a particular sensory system is essential for understanding the cost–benefit trade-offs that have influenced its evolution. This is particularly important when comparing phylogenetically distant species, among which it may not be reasonable to assume that a specific volume of neural tissue consumes similar amounts of energy.

The diversity of energy costs imposed by brains is not limited to sensory units. For example, elasmobranchs have a larger relative brain size compared with teleost fishes of the same body mass, but the overall brain energetic consumptions are similar [64]. A recent study of both vertebrate and invertebrate neural tissues demonstrated that central units also vary in the energy efficiency of information transmission [65]. Honeybee Kenyon cells in the mushroom bodies have an energy efficiency for generating action potentials that are similar to mouse fast-spiking neurons (approx. 40%), but well below the efficiency of mouse thalamo-cortical relay neurons (near 100%). Thus, the energy costs of action potentials in central units also depend on the species and/or the function of the unit.

In the near future, studying the relationships of metabolic costs to cognitive function may be best accomplished through the study of insects. One reason is that it is not possible to generalize on the relationship between brain size and neural density, even with the order

Mammalia [66], and counting the actual number of neurons in different regions of large brains is currently intractable. The small brains of insects, with tractable numbers of neurons, are much more amenable to specific studies of the costs of clusters of neurons.

While fine details such as neural density differences between regions may be difficult to study in vertebrates, the intense decades of effort poured into research on mammalian brains have taught us a great deal about how those regions interact with one another. Recently, Krugel *et al.* [67] described, in humans, an example of a trade-off between two categories of cognitive tasks. Individuals with Val/Val alleles of the catechol-*O*-methyltransferase (COMT) gene performed better in rapid-learning tasks, while those with Met/Met alleles perform better in executive function tasks. The trade-off seems to be rooted in how each task is affected differently by dopamine metabolism level, which in turn is dependent on the COMT. The insect brain is ripe for such investigation because: (i) lower levels of unit replication, than observed in vertebrates, may allow better delineation of individual units and therefore easier identification and manipulation of interactions between units [57], and (ii) information storage appears to occur in specialized pathways opposed to the more general memory storage circuits in vertebrates [68].

3. EXPERIMENTAL EVIDENCE FOR A COST OF LEARNING AND MEMORY IN INSECTS
Regardless of the form of the relationship between brain size, cognitive ability and metabolic costs, some experimental studies have directly addressed the question of the cost of learning and memory in insects. Costs of learning and memory are usually classified as constitutive or induced.

(a) *Constitutive costs of learning*
Constitutive (or global) costs of learning are paid by individuals with genetically high-learning ability, whether or not they actually exercise this ability. They can be seen as pleiotropic effects of genes that improve learning ability. Such effects may be owing to the development and maintenance costs of the neural structures involved in learning and memory [7]. As natural populations face a harsh existence, this extra energy expenditure should be reflected in reduction of survival or fecundity: energy and proteins invested in the brain cannot be invested into eggs, somatic growth or the immune system. Hence, learning ability is expected to show evolutionary trade-offs with some other fitness-related traits. A standard approach to studying evolutionary trade-offs between different traits contributing to fitness is to apply selection to one trait in the direction of increased fitness and observe if the other trait changes in the direction of reduced fitness [69,70]. Mery & Kawecki [71] applied this approach and observed a genetic trade-off between learning ability and larval competitive ability. Larvae from lines selected for improved learning over several generations have a lower larval competitive ability than control lines when food is limited, but not otherwise. The lower competitive ability of the experimental lines is apparently not owing to inbreeding; rather, it seems to be a correlated response to selection on learning ability.

Interestingly, the relationship between learning ability and larval competitive ability appears to be symmetrical. Kolss & Kawecki [72] artificially selected flies for adaptation to larval nutritional stress over several generations and observed a decrease of learning ability in selected lines when compared with control lines. Using a similar approach, Burger *et al.* [73] described a symmetrical trade-off in *Drosophila* between learning ability and adult longevity. By contrast, a recent study [74] showed a positive relationship in honeybees between learning ability and resistance to oxidative stress resistance, which is often related to overall longevity, and *Bombus terrestris* shows a positive relationship between learning ability and antibacterial immune response at the colony level [75]. Taken together, these studies suggest that there are constitutive trade-offs between learning ability and other life-history traits, and that these trade-offs are not fixed but are likely to depend on genetic and environmental factors.

(b) *Induced cost of learning*
The process of learning itself may also impose additional costs reflecting the time, energy and other resources used. This hypothesis predicts that an individual who is exercising its learning ability should show a reduction in some fitness component(s), relative to an individual of the same genotype who does not have to learn. Mery & Kawecki [76] addressed this hypothesis using flies previously selected for increased learning over several generations. Control and selected adult flies, which differed in their learning ability, were kept over several days under environmental conditions in which they could alternatively learn to select for one of two specific oviposition media. In selected lines, the repeated cycles of conditioning caused an increasing reduction of realized fecundity compared with flies not exposed to conditioning; after over 20 days of conditioning the reduction was over 40 per cent. By contrast, when exposed to conditioning, flies from the control lines laid on average about 15 per cent fewer eggs than their non-conditioned counterparts, irrespective of time since the beginning of the assay. These results indicate that the process of learning itself may have a measurable cost in terms of fitness components.

The questions regarding the induced costs of learning and memory are not only restricted to the cost of 'how much' information is processed, but also to 'how' they are processed. Findings from both vertebrate and invertebrate behavioural pharmacology have challenged the traditional view of memory formation as a direct flow from short-term to long-term storage [77–79]. Different components of memory emerge at different times after the event to be memorized has taken place. These findings raise the question of the functional and evolutionary relationships among these different components of memory. As an example, in *Drosophila*, two different forms of consolidated memory have been observed: anaesthesia resistant memory (ARM) and long-term memory (LTM, [80]). These two forms can be independently induced depending on the classical conditioning protocol. Mery & Kawecki [5] studied how specific induction of one consolidated memory affects resistance of adult flies to extreme stress imposed by

absence of food and water. Results indicated that the formation of an LTM in flies reduces their resistance to extreme stress, whereas the formation of an ARM does not. This suggests that induced costs of learning might also be specific to the type of memory formed. Interestingly, in aversive classical olfactory conditioning in *Drosophila*, an LTM is only formed after repeated training events separated in time whereas an ARM is formed after one or multiple training events not separated in time. Such mechanisms may insure that only relevant information, which has been acquired over several independent occasions, would be stored into 'costly' LTM memory, whereas less reliable information would be stored into less expensive ARM memory.

Altogether, these studies suggest that learning and memory carry fitness constitutive and induced costs. However, evidence is still scarce and a better understanding of the nature of the fitness cost of learning and memory clearly requires research on the natural variation in the different memory components, as well as its genetic and neural bases. The notion of a clear separation between constitutive versus induced costs of learning and memory may also be partially misleading. Constitutive costs could be more important than induced costs as induced costs are only present when learning occurs (i.e. when the benefits of learning are supposed to be present [81]). However, the brain is an extremely plastic organ and a single experience can modify its structure permanently. Thus, even a single experience may have induced costs in the short term as well as constitutive costs in the long term. These two forms of costs may be difficult to disentangle experimentally, but examining them may reveal new and interesting challenges that lead to a better understanding of the evolution of cognition.

(c) *Information processing versus storage costs of learning and memory*

The literature on the costs of learning and memory is mainly focused on the costs of learning rate or memory abilities. However, the amount of information that can be stored in a brain—even the small brains of insects—greatly exceeds the simple training procedures usually conducted under laboratory conditions [82]. In nature, animals can face spurious or contradictory information, and may have to combine different kinds of information. Variation in information processing among animals may reveal some fitness costs of learning and memory. For instance, information about the current environment has to be constantly updated whereas out-of-date information has to be disregarded or forgotten. Models of adaptive forgetting have been developed and describe a link between optimal memory and environmental heterogeneity [83–85]. The evolution of optimal memory requires a certain level of environmental stability between generations, and these models may explain the adaptive separation between an ARM and LTM as described above. However, these models do not include general cognitive processes, such as interference, reversal learning, reconsolidation or extinction, which may strongly participate in the updating of information independently of the level of environmental heterogeneity [86–88].

How outdated information is dealt with is still controversial. Is it erased or hidden? Current knowledge on reconsolidation and extinction in bees [89,90] and *Drosophila* [91] suggests that old memories are not eliminated but only hidden by updated information. How memories are coordinated and managed requires more study. As with storing information, erasing information might also be costly because it is energetically demanding and risky [89]. The complete and unique elimination of an outdated memory, without interfering with needed information, may exceed the cost of keeping all memories. We still know very little on the organization of information processing and how cognitive abilities reflect adaptation to environmental conditions.

Retroactive interference occurs when the retrieval of previously learned information is hindered by more recently acquired information. It may thus be adaptive under strong environmental heterogeneity but costly when the environmental conditions rarely change. A recent study [92] described, in *Drosophila*, genetic variation for retroactive interference in a single gene (*foraging*) that is associated with natural variation in the foraging behaviour. One allelic variant, called *rover*, move more rapidly through their foraging environment when compared with the other variant, called *sitter*, and may thus experience greater environmental heterogeneity. Individuals with a *rover* allele also show greater retroactive interference compared with individuals who are homozygous for the *sitter* allele, which might be an adaptive response to this difference in environmental heterogeneity. The costs of information processing thus depend on both the environment and the genotype. The resulting cost may be maladaptive behaviour, given the particular environment. Clearly, more work is required to understand the genetic and environmental variation in information processing.

4. CONCLUSION

The studies we have described, conducted in the miniature brains of insects, demonstrate that the relationships between brain size, learning ability and costs are not straightforward. Smaller brained animals often differ only in quantitative abilities rather than qualitatively from larger brained animals. Different types of neural units display ample variation in their metabolic cost, independently of their size. Future lessons from insect brains could come from the study of the metabolic costs of higher order processing units in insects varying in their reliance on visual or olfactory inputs. We need to also consider, though, that measurements of biophysical performance are not measurements of fitness. The study of the induced energy costs of central units, such as the mushroom body when it is used during a learning situation, could help us get a step closer to actual reproductive fitness. Despite (or perhaps because of) strong interest, research on the costs of learning and memory has yielded more questions than answers. Understanding the evolution of learning and memory will require the integration of neurobiology, behavioural ecology, population genetics, developmental biology and evolutionary biology; the study of the 'mini-brains' of insects has huge potential to make these links.

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