

# The complexity of learning, memory and neural processes in an evolutionary ecological context

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The ability to learn and form memories is widespread among insects, but there exists considerable natural variation between species and populations in these traits. Variation manifests itself in the way information is stored in different memory forms. This review focuses on ecological factors such as environmental information, spatial aspects of foraging behavior and resource distribution that drive the evolution of this natural variation and discusses the role of different genes and neural networks. We conclude that at the level of individual, population or species, insect learning and memory cannot be described as good or bad. Rather, we argue that insects evolve tailor-made learning and memory types; they gate learned information into memories with high or low persistence. This way, they are prepared to learn and form memory to optimally deal with the specific ecologies of their foraging environments.

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The use of previous experience to optimize behavior in an adaptive manner is obviously of great benefit to all animals, including insects [1,2]. However, this does not mean that insects should learn and remember information from all possible experiences they encounter. Studies on diverse insect species have revealed the daunting complexity of different forms of memory each with different stabilities, including short-term memory, mid-term memory, anesthesia-resistant memory and long-term memory (STM, MTM, ARM and LTM), for example [3–6]. In [Figure 1](#) we provide a basic description of these memory forms and their abbreviations. Why does learning not always result in the formation of LTM? To ensure the reliability of learned information, most animals require multiple, spaced experiences before information is stored

as LTM. Nevertheless, some animals form LTM after a single experience suggesting that they may have evolved to rely on the value of the learned information more readily than other animals, rather their having evolved superior learning and memory abilities [7]. Several factors have been described that play a role in learning and memory including the high energetic costs of memory formation [8,9], the effects of age, physiological state, longevity, stress and the number of lifetime experiences [10–13,14\*].

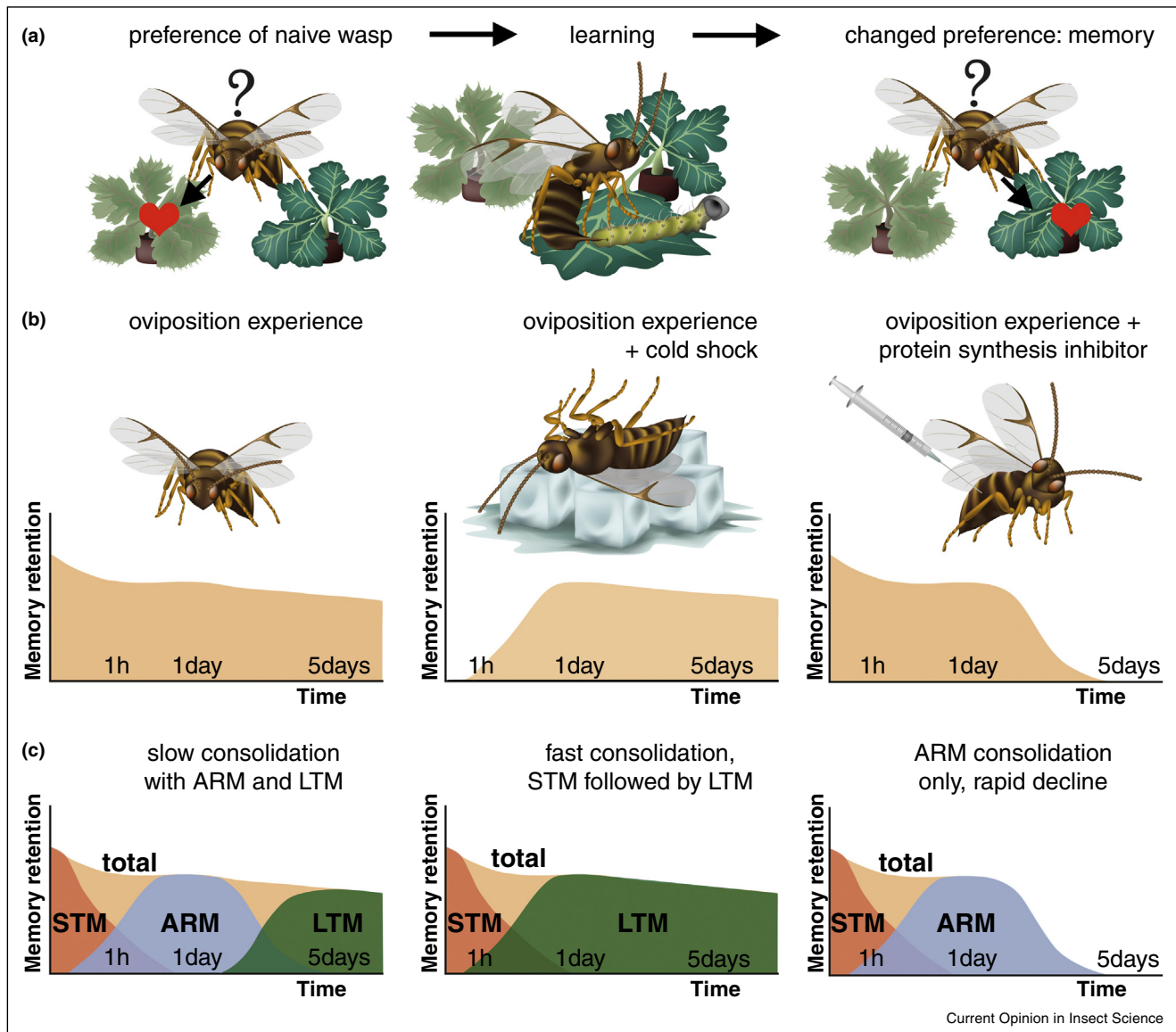
This review focuses on aspects of variation in the importance and reliability of the learned information. An animal must continuously be able to adjust its behavior according to previous experiences, but only if that experience is still relevant at the time of memory retrieval. Thus, insects evolve preparedness to learn and form memories in a manner that is adaptive in the context of their specific ecology. The term prepared learning [15\*] is used in this review to describe preparedness to learn (for instance to learn odors more easily than colors) but also preparedness to gate the learned information into specific forms of memory that differ in stability (for instance in MTM or in LTM). Below we will describe recent advances in studies that focus on ecological factors driving natural variation in prepared learning.

## Effects of environmental variation and spatial foraging behavior

Environmental variation has been proposed as one of the major factors driving the evolution of variation in learning and memory retention [7,16–18]. More variable environments promote short lasting memories, which can be updated continuously. If environmental variation is low, learned information remains relevant for a long time, which favors long lasting memories.

Spatial foraging behavior of the insect influences variation in the perceived environment. An insect that migrates after learning area-specific information does not benefit from LTM formation because the learned information becomes obsolete after migration. This could drive the evolution of differences in prepared learning, because formation of LTM would be more beneficial to insects that stay longer in a certain area than insects that tend to forage over longer distances to areas with very different types of resources. Such variation in prepared learning may have evolved within natural populations of *Drosophila melanogaster* flies (both in larvae and in adults), where so called *rover* flies tend to forage for food over longer

Figure 1



Memory retention can be determined by various behavioral choice assays [34,69], such as depicted in (a), or by measuring conditioned reflexes [48] at different intervals between conditioning and memory retention tests, resulting in a graph as shown in (b) (left panel). This memory is composed of at least three different memory types, uncovered by specific inhibitors are used. Short term memory (STM) can be erased by anesthesia such as cold shock (cooling insects on ice, b mid panel). Long term memory (LTM) requires the production of new proteins and can be inhibited by translation and/or transcription inhibitors (b, right panel). Memory that is not affected by both treatments is anesthesia-resistant memory (ARM). Note that the acronym ARM is used specifically in fly literature, and mid term memory (MTM) or intermediate term memory (ITM) is used as equivalent to ARM in other species. MTM in flies refers to a late phase of STM [70]. STM, ARM and LTM have further been subdivided in early and late forms by other specific inhibitors, see, for example, [4–6]. From the combined results of control, cold shock and protein synthesis inhibitor experiments, memory type graphs can be prepared as shown in (c) (left panel). Here the memory type is shown where first STM is formed (orange), followed by ARM (blue) and LTM (green), with the sum of all memories (observed without inhibiting treatments) depicted as yellow. Variations exist, for instance in the speed of consolidation of LTM and consolidation with or without intermediate ARM (c, left versus mid panel) or in the consolidation of ARM only (c, right panel) [37]. Also, the persistence of memory forms over time can vary between species.

distances, whereas *sitter* flies tend to aggregate and exploit a local food source extensively [19]. This behavior has been shown to result from a single nucleotide polymorphism on a gene encoding a cGMP dependent protein

kinase (PKG), called *foraging* (*for*). *Rover* flies have a higher PKG activity level [20] and experience a much more variable environment than *sitter* flies due to their explorative behavioral lifestyle. The *for* gene has been

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