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Environmental effects on learning behaviour, learning performance and generalisation in honey bees and humans

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1 INTRODUCTION

1.1 ECOLOGY, EVOLUTION, AND LEARNING

The fundamental concepts in ecology are the dependence and interaction of all living organisms with their environment and – of course – other organisms (Ganong 1904; Krebs 1972; Townsend, Begon & Harper 2008). Living in and interacting with an environment determine the physiological and behavioural requirements and abilities an organism has to possess in order to survive in its particular habitat (for an overview see Willmer, Stone & Johnston 2005). This habitat includes both biotic factors such as conspecifics, predators, parasites, competitors and plant matters as well as abiotic (e.g. soil, temperature, humidity, oxygen, day length) factors.

The environment of an organism is usually unstable: Both biotic and abiotic factors which form this environment are subject to often severe and annually recurring changes: examples for these changes are flooding or drying of a habitat, temperature changes, alteration of day length in temperate and polar regions, the sudden occurrence of predators. An organism has to react to these changes both physiologically and on the behavioural level. Examples for physiological adaptations towards a changing environment are hibernation and torpor (Kortner & Geiser 2000), an example for behavioural adaptation is animal migration (Schmidt-Koenig 1975). Examples for both can be found in all groups of animals such as mammals, birds, amphibians, reptiles, insects and other arthropods, and both examples are an adaptation to seasonal changes. The decline of food resources and temperature nearing winter are an annual change which is well predictable due to e.g. change of day length. Organisms can adapt to these predictable, annually recurring changes of a habitat through natural selection. For example, certain species of aphids show a very complex life cycle with seasonal alternation between two disjunct sets of hosts because their primary hosts are usually of poor nutritional value in mid-summer (for an overview see Moran 1992). These (circ-)annual changes affect the whole population; therefore behavioural adaptations underlie natural selection.

For an individual with a limited lifespan, however, natural selection of adaptations is not suitable to react to short-termed environmental changes (Lewontin 1979). Under these circumstances, the ability to learn directly benefits the individual's fitness (Johnston 1982). If the changes of an organism's habitat do not occur regularly and are not predictable, and/or the individual occupies a large variety of habitats, learning offers the individual an opportunity to react to sudden changes of its habitat.

From a teleological point of view, the advantages and benefits of the ability to learn are obvious (Mayley 1996a; 1996b; Johnston 1982):

1) Temporal adaptability is much higher than evolution. A learning species can adapt faster and on the individual level as opposed to a non-learning species which can adapt only on the population level over a greater time course.
2) Also spatial adaptability is better because learning individuals are able to adapt to specific needs of their habitat which might differ only little from the neighbouring habitat for which the population is optimized.
3) At least in songbirds, learning influences sexual selection and therefore increases reproduction (Byers & Kroodsma 2009).
4) Learning might be a superior solution to natural selection. In natural selection, only the currently available variations can compete for resources, even though the adaptations might not display the best solution for the actual situation (or might not be present at all). Learning could cure these deficits by adapting a reasonably successive inherited behaviour with a learned modification.
5) Learning might provide a skill that is simply very hard to evolve. A classical example of this benefit is the learning of a certain language (Pinker 1994).

Taking this into account it is astonishing how many species rely on inherited, genetically programmed behaviour rather than the ability to learn (Davey 1989). But evolution is not teleological, and there are quite large costs and dangers which have to be taken into account (Davey 1989; Mayley 1996a; 1996b):

1) The organism is highly vulnerable during learning because sensory input and information processing are occupied by learning and less vigilant towards predators.
2) The complexity of the nervous system has to be increased to acquire, process and store the information retrieved during learning (Laughlin 2001; Johnston 1982).
3) Reproduction is impaired (Mery & Kawecki 2003).
4) Reproduction might be delayed due to a prolonged childhood during which learning takes place (Johnston 1982).
5) Gaining experience and making mistakes is costly in terms of energy and time (Laverty & Plowright 1988; Dukas & Visscher 1994; Heinsohn 1991).
6) Prolonged postnatal development (“childhood”) coincides with increased parental care (Clutton-Brock 1991; Trillmich 2010)
7) Lifetime is reduced (Burger et al. 2008).
8) Finally, there is the danger of “learning the wrong thing” and being maladapted afterwards (Davey 1989).

These costs seem to outweigh the benefits, thus it seems to be beneficial for most organisms to favour programmed behaviour instead of learning (Davey 1989).
However, to gain a better understanding of the mechanisms underlying animal learning and memory, we have to gather knowledge about the biological requirements of an animal, how the environment creates obstacles for meeting these needs and which strategies could help satisfying them under the given conditions. So the investigation of animal learning and memory has to pose the question which environmental aspects play a role in the development of learning abilities

1.2 INSECT LEARNING

Most phyletic lines which developed the ability to learn are vertebrates, but even though learning is costly and most insects have a very short live span, a few insect taxa have evolved the ability to learn: e.g. phytophagous insects such as caterpillars and grasshoppers can learn to avoid certain food sources (Bernays & Bright 1993; Bernays & Lee 1988; Dethier 1980; Lee & Bernays 1988, 1990), parasitoid wasps learn to distinguish butterflies (Huigens et al. 2009), butterflies learn to distinguish leaf shapes (Allard & Papaj 1996). Among the insects capable of learning, in particular honey bees (Gould 1993), bumble bees (Leadbeater & Chittka 2007a, b), parasitoid wasps (Turlings et al. 1993), and cockroaches were established as insect model systems for the research on insect learning mechanisms (Eisenstein 1997). The fruit fly *Drosophila melanogaster* is widely used as a model system for the neurogenetics of learning (Anholt & Mackay 2004).
Social hymenopterans show highly developed learning abilities due to their life strategy: there is an adaptive value of learning in a “super-organism” like a honey bee hive (Moritz & Southwick 1992). In honey bee or ant nests, individual learning and memory plays an important role. A desert ant such as *Cataglyphis* will leave its nest for foraging and walk dozens of meters in an irregular manner. Nevertheless, after finding a food source, it will return directly to the nest without any detour (Wehner & Menzel 1969). To do that, it must have the ability to

1) learn, memorize and recognize the nest’s location
2) learn, memorize and recognize landmarks, celestial cues such as the E-vector of polarized light and the time of day
3) integrate the location of the nest, its own location in relation to the nest, and the distance and the route between both on an internal map.

The same principles apply to foraging honey bees, bumble bees and wasps. They also remember the position of a food source and return to exploit it completely (Frisch 1965).
To map the current and the nest’s position with the help of celestial cues (see Rossel, Wehner & Lindauer 1978 for honey bees; and Wehner 1989 for desert ants), ants and bees have to take

into account the time of year (and the relative position of the sun to the azimuth), the time of day (and the actual position of the sun to the azimuth) and their position on the earth's surface. Lindauer was able to demonstrate that honey bees know very accurately their position, time of day and what date it is (Lindauer 1957, 1959, 1960). The cue itself (in this case the e-vector of polarized light) for determining the position is used innate, but its relevance, acuity, and usability for a certain task as well as the changes it undergoes during the task must be acquired by learning.

1.3 ECOLOGICAL IMPACTS ON LEARNING AND MEMORY

As outlined above, insects and other animals interact with their environment and have to learn how an environment changes (during one day, during one year) and how they can adapt and react to these changes by behavioural modifications. But the question arises how learning itself may be influenced by the environment and its changes. It is easily comprehensible that a certain task which an animal can or cannot learn has to be connected to its physiological abilities and its needs. Only animals that forage cooperatively need the ability to communicate the location of a resource; solitary animals won't need this skill (Shettleworth 1998). But are there environmental situations which promote or impair learning?

It has been shown in honey bees that there are external factors influencing learning: infection with the parasite *Varroa destructor* impairs learning in honey bees (Kralj et al. 2007); it also has been shown that stress and viruses can decrease the ability to learn of honey bees (Iqbal & Müller 2007; Iqbal 2009).

However, the question whether biotic or abiotic aspects of the honey bees' ***habitat*** might play a role in learning remains unanswered so far. Does learning change with the environmental history and context of the experience? And do history and context alter the honey bees' behaviour; can we measure effects of those experiences on subsequent performance?

1.4 AIM OF THIS STUDY

This work was performed to contribute to the knowledge on the effects of environmental conditions on insect learning and memory. To address this question, learning and memory of honey bees were investigated with respect to several naturally occurring environmental conditions as there are light, circadian rhythm and floral patterns. Additionally, some of the experiments were also conducted in humans to gain a better understanding of the mechanisms underlying the behavioural changes promoted by the environment.

This work will be divided in three main parts:

A) Influence of diurnal rhythms and light on learning in honey bees
B) Generalisation behaviour in honey bees and humans
C) Ecological and evolutionary aspects of learning in invertebrates

In the first part, I investigated whether there is a dependency of honey bee learning performance and the time of day during which a certain task is learned (chapter 2.1). Because there might be a dependency between learning and feeding, I further investigated the possible role of plant diurnal rhythms for honey bee performance and how these diurnal rhythms might retroact on each other (chapter 2.2).
Light is another important environmental factor determining e.g. honey bee foraging behaviour, thus I examined the possible role of different light conditions on honey bee learning and memory (chapter 2.3).
The second part tries to enlighten the role of previous experience on generalisation behaviour. The influence of extended or reduced odour exposition on olfactory generalisation was examined in both honey bees and humans in different behavioural assays. The effect of exposure on generalisation behaviour and the persistence of possible changes (chapter 3.1), the importance of attention for odour perception (chapter 3.2), interactions between perception, generalisation and odour labelling in humans (chapter 3.3) and generalisation behaviour of free-flying honey bees for both visual and olfactory stimuli (chapter 3.4) were investigated.
Because not all bees learn equally well, the third part is more theoretical and deals with the possible adaptive value of non-learning in a social insect, the honey bee. In this part, some of the data presented in the first two parts is reconsidered under a different view, put in a broader context of earlier studies and discusses the possible benefits of non-learning bees for the survival of the colony (chapter 4.2).