

2 Learning: Mechanisms, Ecology, and Evolution

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2.1. Introduction

Learning in humans and other animals was closely examined in a variety of scientific disciplines during the twentieth century. Recently, with the growing awareness that there are remarkable similarities among species ranging from fruit flies to humans, there has been increased integration of ideas and data across traditional disciplines. I attempt to present such an integrative approach to the study of learning in this chapter. I focus on five major questions. First, what is learning? I provide a definition, discuss the difficulties associated with quantifying learning, and briefly outline key genetic and neurobiological mechanisms underlying learning. Second, why learn? To answer, I commence with analyzing life without learning and then detail fitness benefits of learning. Third, who learns? While I suggest that the answer is probably all animals with a nervous system, there is still no empirically based answer to this question. Therefore, I instead focus on examining what an animal has to possess in order to learn and what costs are involved. Fourth, what do animals learn? To illustrate the broad reliance on learning among animals, my answer focuses on a single species, the fruit fly *Drosophila melanogaster*, which learns much more than we had thought. Finally, is learning important? I discuss effects of learning on ecological interactions, the dominant role of learning in the life history of numerous species, and effects of learning on evolutionary change. Although there is a large body of literature on a multitude of features of learning, my interdisciplinary analysis identifies topics requiring further investigation. I thus conclude with a list of such promising future directions.

2.2. What is learning?

2.2.1. DEFINITION AND MEASUREMENTS

Learning may be defined as the acquisition of neuronal representations of new information. That information is then retained for at least a short period (short-term memory) and often for long durations (long-term memory) and

typically influences relevant decisions and behaviors. Examples of learning include neuronal representations of new (*i*) spatial environmental configurations, (*ii*) sensory information including visual, auditory, olfactory, taste, and tactile features, (*iii*) associations between stimuli and environmental states, and (*iv*) motor patterns, for example, the sequence of body movements involved in manipulating a novel food (Dukas 2008a). My above definition refers to explicit neuronal representation of information and hence excludes habituation and sensitization, which are typically considered simple forms of learning.

Although learning involves changes in neuronal activity and configurations, it can currently be quantified only through its effects on behavior. That is, owing to the large number of neurons involved and the distributed nature of neuronal activity, one cannot quantify learning directly through measuring changes in neuronal activity. One can, however, examine the neuronal mechanisms underlying learning and memory (section 2.2.2). Unfortunately, even the quantification of learning through behavior is not a straightforward task. On the one hand, numerous claims for learning in a variety of species have been based on inadequate experiments. Major weaknesses include protocols that could be biased due to the employment of observers not blind to treatments (e.g., R. Rosenthal and Fode 1963) and lack of proper control treatments used to verify that either the presentation of stimuli alone or environmental states alone do not generate behavioral biases that may be misinterpreted as learning (e.g., Alloway 1972). On the other hand, claims for lack of learning in certain species are also problematic because they could merely reflect subjects' failure to engage in behaviors that indicate learning owing to inadequate experimental settings rather than a true inability to learn.

2.2.2. GENETICS AND NEUROBIOLOGY OF LEARNING

The biochemical and genetic architecture underlying learning has been examined primarily in several model systems, including the soil nematode *Caenorhabditis elegans*, the aquatic snail *Aplysia californica*, the fruit fly *Drosophila melanogaster*, the honeybee *Apis mellifera*, and the mouse *Mus musculus*. Obviously, reviewing the immense knowledge acquired over the past few decades is beyond the scope of this chapter. Rather, I will briefly outline key concepts. At the mechanistic level, learning can be perceived as a basic cellular process involving changes in the synaptic properties of neurons. Immediate changes are mediated by neurotransmitters, whereas long-term changes, which involve both biochemical and physical changes in synaptic properties, involve gene expression. The biochemical and structural changes associated with learning

and memory can be studied at the level of individual neurons. Indeed, a few neurons may be sufficient for exhibiting learning in tiny animals such as *C. elegans* (section 2.4.1). Typically, however, learning involves synchronous modulation of numerous neurons, each with specific sensitivities to a variety of environmental features (Kandel et al. 1995; Dubnau et al. 2003).

The dynamics of learning has been elegantly dissected using genetic mutants in fruit flies, but remarkably similar mechanisms underlie learning in all animals, including humans. There are two mechanistically distinct forms of consolidated memory. Anesthesia-resistant memory (ARM) can be formed even after a single training session. It does not require protein synthesis and is relatively short lasting (~24 hours). The path leading to long-term memory (LTM) begins with learning that requires spaced training, meaning that flies require a series of training sessions separated by breaks. The flies then form short-term memory (STM) and medium-term memory (MTM) lasting about 1 and 5 hours respectively. That memory consolidates via a process involving protein synthesis to LTM lasting several days (Dubnau et al. 2003).

In short, many of the genes, biochemical pathways, and structural changes underlying learning and memory have been elucidated. At the level of individual neurons, learning is controlled by several hundred genes and a similar number of biochemicals. Typically, neuronal representations of the environment require the synchronous activity of numerous neurons. This aspect of learning is challenging to quantify owing to the large numbers of cells and connections involved.

2.3. Why learn?

A variety of misleading assertions have linked learning to variation and unpredictability. To clarify the confusion on this topic and answer the question of when animals should learn, I will start by examining the null model of life without learning.

2.3.1. LIFE WITHOUT LEARNING

Most or all organisms experience variation and unpredictability in their external and internal environment. The most fundamental and universal mechanism for handling variation and unpredictability is gene regulation. For example, *Escherichia coli* bacteria can alter gene expression to generate energy from the locally available sugar. If glucose becomes unavailable, the bacteria can activate alternate sets of genes that allow them to exploit several other sugars as their energy source. Furthermore, when their environment lacks a

necessary amino acid, *E. coli* can produce the required enzymes for synthesizing that amino acid (Pierce 2002). In addition to staying stationary and adjusting to the changing environment, *E. coli* and other bacteria can also respond to environmental changes through chemotaxis. This involves a sophisticated system of information processing and behavioral machinery that enables bacteria to move toward energy sources and away from noxious chemicals (Koshland 1980; Eisenbach and Lengeler 2004).

Bacteria can obviously benefit from responding to a change in the environment by seeking better conditions. They would also benefit, however, from modulating their response if they subsequently fail to locate better settings. Indeed, the genetic networks underlying chemotaxis are sensitive to change in the environment rather than to the absolute condition. For example, transferring bacteria from a dish with high glucose concentration to a dish with low glucose concentration causes a change in their movement pattern, which, after a short period, rebounds to the baseline level (Koshland 1980). That is, the bacteria adjust to the new conditions.

Larger and more mobile single-cell organisms such as *Paramecium* can sense and respond to a broader range of environmental variables and exhibit chemotaxis, thermotaxis, geotaxis, and thigmotaxis (movement in response to touch) (Jennings 1906; Saimi and Kung 1987). For example, a *Paramecium* accelerates its forward movement if touched from behind, and it stops and alters its swimming direction if its forward movement is obstructed. The perception of environmental variables and the control of movements are mediated by electrical signaling generated by ion movement across the cell membrane. Similar electrical signaling is also employed by the nervous systems of all multicellular organisms (Eckert 1972; Shelton 1982; P. Anderson 1989; Greenspan 2006; Meech and Mackie 2007). Behavior mediated via electric signaling can also be modulated. Neuronal modulation involves short- and long-term changes in synaptic properties mediated by neurotransmitters and gene expression. Simple forms of neuronal modulation allow animals to either habituate or sensitize to some environmental change. Such modulation can be seen as an ancestral type of learning.

In sum, genetic regulation and behavioral modification underlie organismal response to environmental variation. Whereas bacteria, owing to their small cell size, can rely on chemical diffusion for behavioral coordination and decisions, large single-cell organisms also employ electrical communication to allow fast responses to environmental changes. Multicellular organisms rely heavily on intercellular electrical communication provided by their nervous system to coordinate responses to environmental variation. Both the genetic and electrically mediated behavioral responses can be modulated. That is, even

organisms that do not learn are highly adept at responding to and modulating their responses to variable and unpredictable environments.

2.3.2. ADAPTIVE SIGNIFICANCE OF LEARNING

The fundamental biological ability to modulate genetic and electrical activity (section 2.3.1) is the precursor for learning, which can be perceived as a coordinated neuronal modulation resulting in neuronal representation of information (section 2.2.1). Learning enables individuals to exploit environmental features that are unique to a certain time and place. Animals' ability to learn about such features expands the type and amount of information they can respond to and, consequently, their behavioral repertoire. For example, a bee can acquire a neuronal representation of her nest location, record the spatial location, odor, and color of the best flowers to forage on, and learn a new motor pattern for handling these flowers. And individuals in many species gain from learning to identify their parents, neighbors, potential mates, offspring, and competitors. One can readily imagine how every organism can benefit from learning. Indeed, learning is probably a universal property of all or most animals with a nervous system.

Although one would expect learning to be adaptive, little research has been devoted to quantifying the fitness consequences of learning. In an experiment examining this issue, grasshoppers (*Schistocerca americana*) were assigned to two groups, each receiving two synthetic foods. One food contained the optimal proportion of all nutrients essential to grasshopper growth, while the other was carbohydrate deficient. Subjects in the learning group could associate each of the two foods with distinct tastes, colors, and spatial locations. Subjects in the random group, however, had the food-cue associations assigned randomly twice a day so they could not learn to associate the cues with specific food. The learning grasshoppers rapidly learned to restrict their visits to the nutritionally balanced food, whereas the random grasshoppers kept visiting each food dish at equal frequencies. The random grasshoppers, however, gradually increased the proportion of time spent feeding on the balanced food, suggesting that they relied on a nonlearning mechanism such as a change in taste-receptor sensitivity (Abisgold and Simpson 1988; Simpson and Raubenheimer 2000). Nevertheless, the overall feeding duration on the balanced diet was over 99% for the learning grasshoppers but only 87% for the random grasshoppers (fig. 2.1a). Moreover, the random grasshoppers did not feed on the balanced food as regularly as the learning grasshoppers did, because they approached equally often the dish with the deficient diet. Such an approach typically resulted in brief feeding followed by resting. The behavioral differences between the treatments translated into a 20% higher growth

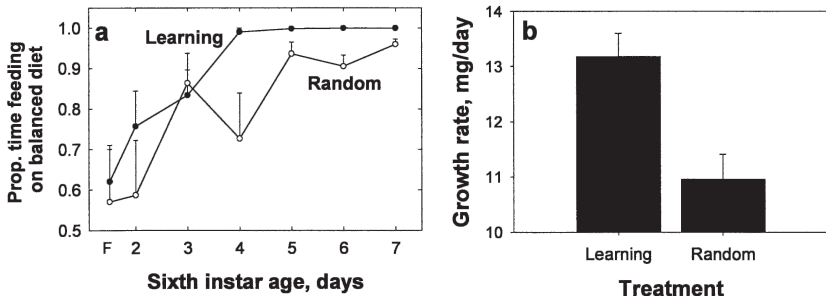


FIGURE 2.1. a. The proportion of time (mean \pm 1 SE) spent at the dish containing nutritionally balanced food by sixth-instar grasshoppers belonging to the random and learning treatments (“F” on the x-axis refers to the first recorded meal). b. The average growth rate of grasshoppers belonging to the random and learning treatments. Data from Dukas and Bernays 2000.

rate in the learning grasshoppers (fig. 2.1b). It is likely that the fitness benefit from learning would be significant also in natural settings, where learning could also translate into less travel and hence lower mortality due to predation (Dukas and Bernays 2000).

2.4. Who learns?

My definition of learning (section 2.2.1), which includes the term “neuronal representations,” conveniently restricts it to animals with nervous systems. Among such animals, learning is perhaps a universal property. It would be difficult to conclude that some animals with nervous systems do not possess learning abilities because of the high odds of obtaining negative results in experiments to detect learning, especially in species we are not very familiar with (section 2.2.1). Because we cannot state which animals with nervous systems do not learn, I will focus instead on examining two features that can determine the prevalence of learning among animals with nervous systems. These features are the biological requirements for learning and the costs of learning.

2.4.1. THE HARDWARE REQUIREMENTS FOR LEARNING

The most essential prerequisites for learning are the abilities to sense some features of the environment and to modulate cellular responses to these features. Because all or most organisms possess these two characteristics (section 2.3.1), all animals with nervous systems may have the potential to learn. This includes even organisms with a small number of neurons such as the soil nematode *C. elegans*, which was chosen over 30 years ago as a simple model

system for examining the structure of a whole nervous system and the way it generates behavior (Brenner 1974). Each hermaphrodite *C. elegans* worm comprises 959 cells, of which 302 are neurons and 56 are glial and other types of support cells. The morphology of each neuron and its chemical synapses and gap junctions has been mapped, and most neurons have been assigned a presumed function. The neurons contain many of the neurotransmitters known in other animals, including serotonin, dopamine, glutamate, acetylcholine, and gamma-aminobutyric acid (GABA) (de Bono and Maricq 2005).

Researchers began to document learning in *C. elegans* in the 1990s. For example, Wen et al. (1997) exposed *C. elegans* worms to either sodium ions or chloride ions with food (a suspension of *E. coli* bacteria) and the alternate ions with no food. In the test following training, worms exhibited a strong preference for the ions previously associated with food, whereas worms in the control groups showed no preference (fig. 2.2). In further experiments, Wen et al. (1997) documented aversion learning and, in two mutants, loss of learning. Using an ecologically relevant assay, Y. Zhang et al. (2005) documented aversive learning to pathogenic bacteria in *C. elegans* and examined the neuronal and biochemical pathways that underlie this learning. Their analyses suggest that changes in a few neurons may be sufficient for the expression of learning (Quinn 2005).

In sum, *C. elegans* illustrates that a nervous system consisting of only 302 neurons can generate learning. The exact set of all biochemical requirements for learning is unknown. However, the neurotransmitters and enzymes that have been determined to mediate learning are involved in other behaviors and cellular processes and are widespread among animals (Bargmann 1998; de Bono and Maricq 2005). Hence, it seems that all animals with nervous systems have the potential to learn. To convincingly falsify the prediction that

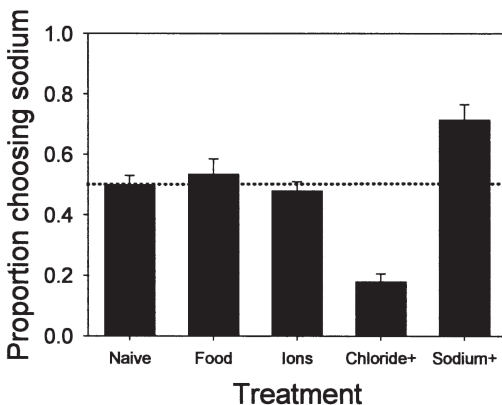


FIGURE 2.2. Learning in *C. elegans* worms. Naive worms, worms exposed to food alone, and worms exposed to sodium and chloride ions alone exhibited no significant preference for either chemical in the following test, whereas worms exposed to one ion with food and the other with no food significantly preferred the ion associated with food in the test ($P < 0.05$). Data from Wen et al. 1997.

all animals with nervous systems learn, we would require strong converging behavioral and neurogenetic evidence, with the latter identifying the precise features that allow an animal to generate complex behavior but no learning.

2.4.2. COSTS OF LEARNING

The acquisition, retention, and use of information by animals cannot be cost free. Because the cost of biological information has been primarily studied in the context of gene regulation, I will briefly discuss errors and their control in the genetic system. There are key similarities between the genetic and nervous systems. Most notably, both genetic regulation and neuronal control involve coordinated networks of individual units with no central management, and genes and neurons may belong to more than one network, each regulating a distinct function. Furthermore, because genes determine neuronal structure and activity, genetic errors can directly translate into errors in neuronal networks (Dukas 1999a).

The maintenance of genetic information is prone to error because DNA is subjected to high rates of damage, which could interfere with DNA replication and transcription (Kirkwood et al. 1986; Bernstein and Bernstein 1991). Both gene transcription and translation into proteins are also prone to error, owing mostly to the stochastic nature of biochemical reactions that depend on infrequent events involving a small number of molecules. A few mechanisms that help reduce either the errors or damage caused by errors include extensive redundancy, active enzymatic correction of DNA damage, a variety of feedback loops, and optimal rates of transcription and translation that minimize error (Raser and O'Shea 2005). All the mechanisms just mentioned come at a cost. Redundancy implies that cells produce and maintain more DNA, genes, RNA, and enzymes than the minimum required. Similarly, possessing regulatory circuits increases the number of genes, RNA, and enzymes. Enzymatic correction of DNA damage is energetically expensive, and because frequent transcription followed by inefficient translation results in lower noise than infrequent transcription and efficient translation, cells incur an extra energetic cost associated with excess production of mRNA (Rao et al. 2002; Raser and O'Shea 2005).

Perhaps the most vivid illustration of the trade-off between accuracy and cost comes from research on variants of DNA polymerase in phage T4. First, an increase in DNA polymerase accuracy is associated with an exponential increase in energy expenditure and a decrease in the rate of DNA synthesis. Second, wild-type polymerase is not as accurate as a few available mutants, suggesting that the wild type possesses the optimal balance between accuracy and cost (Bessman et al. 1974; Galas and Branscomb 1978; Galas et al. 1986).

In sum, the genetic system is prone to errors and contains a variety of costly error correction mechanisms, which reduce but do not eliminate errors.

Learning results in at least STM and often LTM. STM involves chemical changes in synaptic properties, and LTM requires gene transcription and translation into proteins (section 2.2.2). As just discussed, these processes are affected by genetic errors. It is possible that gene regulation in some parts of the brain is subjected to higher standards of accuracy coupled with higher metabolic costs. An alternative means of reducing the effect of errors is through redundancy in neuronal networks, which is also associated with higher costs of developing and maintaining additional, metabolically expensive brain tissue (Dukas 1999a). Also, synaptic transmission is unreliable, meaning that only fewer than half of the presynaptic impulses arriving in a synapse produce a postsynaptic response. The limiting factor is the stochastic nature of neurotransmitter release processes, which involve either a small number of release sites or a low probability of neurotransmitter release per site (Allen and Stevens 1994). The simplest way of compensating for synaptic unreliability is through extensive redundancy. For example, in pyramidal neurons of the rat hippocampus, the synchronous activity of several dozen synapses is necessary to produce a spike train (Allen and Stevens 1994).

The only direct evidence for the costs of learning and memory comes from a series of experiments with fruit flies (*D. melanogaster*). In one study, Mery and Kawecki (2003) found that artificial selection on learning ability in adult flies, which increased learning scores in the selected lines, was associated with reduced larval competitive ability when food was limited. In another study, Mery and Kawecki (2004) exposed food-limited adult flies to alternating substrate conditions, which required use of learning for substrate choice every other day. Under these conditions, flies from lines selected for improved learning ability exhibited lower egg-laying rates than flies from unselected lines. Finally, Mery and Kawecki (2005) documented in flies selected for enhanced learning ability that, compared with a few control treatments, flies that were subjected to a training regime that produced LTM showed earlier death under starvation and dehydration (fig. 2.3). This set of experiments suggests that, at least in flies with artificially selected enhanced learning ability, both learning and memory have significant physiological costs.

In addition to the structural and physiological costs just discussed, learning has ecological costs associated with inexperience. That is, in many species, inexperienced, typically young individuals incur very high mortality rates owing to a combination of deficient feeding techniques and antipredatory behavior (reviewed in Dukas 1998c). For example, recently independent juvenile yellow-eyed juncos (*Junco phaeonotus*) were about one-third as proficient

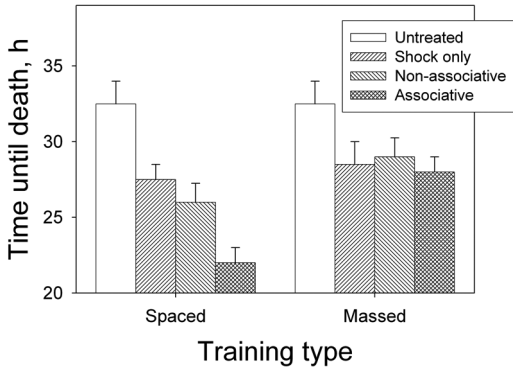


FIGURE 2.3. Costs of long-term memory. Female fruit flies subjected to training that produced long-term memory (associative conditioning with spaced training) had higher mortality rates when kept with no food and water than all other treatments that produced either anesthesia-resistant memory (with massed training) or no memory (untreated, shock only, and nonassociative conditioning with spaced training). Data from Mery and Kawecki 2005.

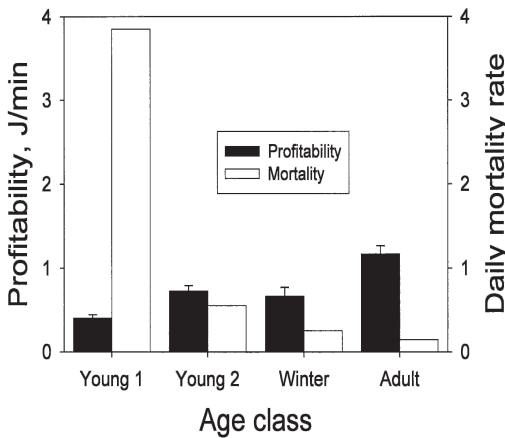


FIGURE 2.4. Effects of experience on feeding proficiency (the profitability of large mealworms) and mortality rate in yellow-eyed juncos. Age classes: recently independent juveniles (Young 1), young experienced juveniles (Young 2), old experienced juveniles during the fall and winter (Winter), and adults over a year old (Adults). Data from K. Sullivan 1988a, 1988b, 1989.

at handling large mealworms as adults. The juveniles spent over 90% of the day foraging and had mortality rates that were over 20 times higher than those of adults, who fed for only 30% of the day (K. Sullivan 1988a, 1988b, 1989). The gradual improvement in feeding proficiency and, probably, antipredatory behavior lasted several months (fig. 2.4). Similarly, independent juvenile European shags (*Phalacrocorax aristotelis*) compensated for low proficiency in capturing fish by spending up to twice as much time as adults foraging until constrained by short day length in late fall. Insufficient feeding during the short winter days was probably the major cause for the high juvenile winter mortality rate, which was five times that of adults (Daunt et al. 2007). The ecological cost of inexperience, however, has to be viewed in perspective: learning allows animals to exploit environmental features, behavioral repertoire, and niches that cannot be used otherwise (section 2.3.2). So the initial period of inexperience can be seen as a necessary component of a life history that relies on and ultimately benefits from learning (section 2.6.2).

2.5. What do animals learn?

Early studies of animal behavior emphasized the importance of instinct in most nonhuman animals and insects in particular (Fabre et al. 1918; Tinbergen 1951). Such views still dominate in many disciplines of ecology and evolution. Two related events that have been instrumental in changing our current understanding of learning are the highly successful establishment of fruit flies as a model system for research on the neurogenetics of learning and the realization that the genetic and cellular mechanisms controlling learning and memory are remarkably similar across diverse taxa. Intriguingly, although evolutionary biologists have studied fruit flies for about a century (Kohler 1994), it was neurogeneticists who critically documented robust learning in *Drosophila melanogaster* (Quinn et al. 1974; Davis 2005). The neurogenetic work on learning in fruit flies has required the development of behavioral protocols for quantifying learning. Consequently, a variety of ingenious procedures have been developed in the past few decades, which indicate that fruit flies rely on learning for all major life activities.

I will focus on fruit flies in this section because they possess a few characteristics that raise the question as to whether they should learn at all. First, fruit flies *D. melanogaster* are tiny, short-lived animals. The adult female is only about 2.5 millimeters long, and the male is slightly smaller. Larval development takes about 4 days (Ashburner et al. 1976), and adults in the wild probably have a life expectancy of only several days. Second, the larval and adult brains contain approximately 20,000 and 200,000 neurons respectively. These are remarkably small numbers compared with vertebrates. Finally, fruit fly life history appears straightforward and does not readily indicate reliance on learning. In fact, we still do not know to what extent fruit flies depend on learning in natural settings because all research relevant to learning has thus far been conducted in the laboratory.

Female fruit flies lay their eggs on decaying fruit containing yeast. Hence, upon emergence, the larvae just have to commence feeding, which is their sole task. Even though the larval task seems easy and they possess limited sensory and information-processing abilities, larvae are able to learn. In the first documentation of learning in fruit fly larvae, Aceves-Pina and Quinn (1979) allowed groups of third-instar larvae to experience three 30-second pulses of one odor together with the application of an electric shock. The larvae also experienced three 30-second pulses of another odor not associated with shock. The two treatments were alternated and separated by 90-second breaks. In a subsequent choice test, the larvae exhibited significant avoidance of the odor associated with shock. Control treatments employing the application of only odorants or only shocks indicated no effects of these nonassociative treatments

on odorant choice. Furthermore, larvae from learning-deficient mutant lines failed to show associative learning (Aceves-Pina and Quinn 1979).

The documentation of learning in fruit fly larvae raised the question of whether such learning ability may contribute to fitness in natural settings. To explore this issue, I tested for associative learning of ecologically relevant tasks in fly larvae. Groups of larvae learned to prefer odors associated with high-quality food and to avoid odors associated with disturbance caused by simulated predation. The larvae, however, did not show significant learning of odors associated with optimal temperature (Dukas 1999b). In further experiments, Gerber et al. (2004) associated two illumination conditions (light and dark) with sugar and one of two negative reinforcers: quinine and table salt. Experienced larvae, which were tested individually, preferred the illumination associated with sugar. In sum, fruit fly larvae can learn to associate either odors or light conditions with the two types of environmental states most relevant to the larval stage, which are food quality and danger. One can readily imagine that there is substantial variation in food quality and danger within a fruit and between adjacent fruits in nature, that such variation is associated with odor or lighting, and that larvae can gain from learning about and seeking stimuli associated with higher growth rate and survival.

Like the larvae, adult fruit flies can learn to avoid odors associated with electric shock (Quinn et al. 1974) and to prefer odors associated with food (Tempel et al. 1983). The adults can also learn to avoid light sources of distinct frequencies associated with aversive states (shock or violent shaking) (Quinn et al. 1974; Folkers 1982) and to avoid flying toward visual patterns associated with high temperature (Wolf and Heisenberg 1991; G. Liu et al. 2006). In short, adult fruit flies can learn about odors, colors, and visual patterns associated with either positive or negative outcomes.

Both male and female fruit flies also learn in the context of sexual behavior. The original protocol for learning in the context of courtship involved males that courted recently mated, unreceptive females for one hour. Compared to inexperienced males, the experienced males exhibited reduced courtship of immobilized virgin females (Siegel and Hall 1979). Further experiments indicated that the males learn to associate the failure to mate with specific female pheromones (Ejima et al. 2005). Experiments involving more naturalistic settings and no immobilized test females indicated that male learning is adaptive: experience with courting unreceptive, recently mated females caused males to selectively reduce subsequent courtship of mated females but not virgin females. The experienced males were also faster to approach virgin females during the test and slower to respond to mated females than inexperienced males

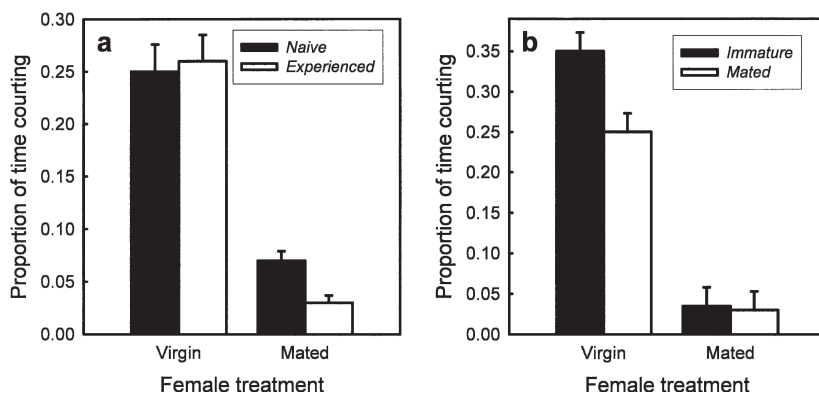


FIGURE 2.5. The proportion of time (mean \pm 1 SE) male fruit flies with distinct experiences spent courting either virgin or recently mated females. In panel a, the males were either naive (black bars) or experienced at courting mated females (white bars). In panel b, the males experienced either immature females (black bars) or mated females (white bars). Data from Dukas 2005a.

were. In another experiment, experience with courting unreceptive, immature females caused males to selectively increase subsequent courtship of virgin females but not mated females (fig. 2.5). In this case, the information about the imminent availability of virgin females caused the experienced males to approach either female type faster than inexperienced males (Dukas 2005a).

Much of the work on learning in the context of courtship in fruit flies has been restricted to males. Females, however, have ample opportunities for learning about potential mates and rely on such learning to improve mate choice. Most notably, although it takes females one to two days to reach sexual maturity, during that time immature females are courted vigorously by many males (Dukas 2006). When immature female fruit flies experienced courtship only by small males, which are less desirable mates than large males, the females subsequently were more likely to mate with small males than females that had experienced courtship by large males (Dukas 2005b). That is, when the females learned that only small males were available, they were less likely to reject small males as mates.

Male fruit flies also seem to learn in the context of aggression. In the field, males defend territories containing decaying fruit and females. Larger males are more likely to hold territories and have a higher mating success (Markow 1988). In laboratory trials, males rapidly establish dominance hierarchy based on fighting, with the winner remaining at a food cup containing a female while the loser retreats. When a loser in one match was allowed to rest for 30 minutes

and then either rematched with the familiar winner from the first match or matched with an unfamiliar winner from another match, losers lunged significantly more often toward unfamiliar than familiar winners (Yurkovic et al. 2006). Individual recognition could be beneficial for both males and females also in the context of courtship and mate choice. For example, a male could benefit from learning to avoid a female that has recently rejected him. Published evidence to date, however, indicates only that male fruit flies can learn to distinguish among categories of females of distinct reproductive state (Ejima et al. 2005). Nevertheless, individual recognition is known in other insects (Dukas 2008a) and invertebrates (e.g., Gherardi and Tiedemann 2004; Detto et al. 2006) and is ubiquitous in vertebrates (see Beecher and Burt, chapter 4 in this volume).

The extensive work on fruit fly learning is highly illuminating because they employ learning in all four central behavioral categories of feeding, predator avoidance, aggression, and sexual behavior. It is almost certain that fruit flies do not possess exceptional learning abilities relative to other animals. Rather, they have been studied closely. Hence, it would be sensible to assume that most other animals also rely on learning in all central domains of life. Similarly, it is likely that vertebrates such as birds, which have larger brains and life expectancies of a few years, possess elaborate learning and memory abilities. Overall, it appears that the magnitudes of learning and memory abilities in nonhuman animals have been underestimated despite their potentially broad influences on animal behavior, ecology, and evolution.

2.6. Is learning important?

Learning affects all major ecological and evolutionary processes in animals, but this has been underappreciated owing to the difficulty of quantifying learning and its influence.

2.6.1. ECOLOGICAL SIGNIFICANCE OF LEARNING

As illustrated in section 2.5, most ecological interactions in most animals involve learning. Learning affects patterns of competition, predation, and antipredatory behavior, and it can determine levels of immigration and emigration. Perhaps most fundamentally, the ability to learn has opened up numerous niches unavailable otherwise. For example, unlike many solitary wasps and bees, which specialize on one or a few food types, social hymenoptera have several generations per year. This means that, owing to seasonal variation, individuals must learn about the best food available at their place and time. That is, the ability to learn was probably a precondition for the evo-

lution of sociality in ants, wasps, and bees. Extensive learning is also required in all species consuming prey that is challenging to capture or handle. This category includes many species of birds and mammals and numerous other taxa. Examples include fish-eating birds (e.g., Daunt et al. 2007), oystercatchers (Norton-Griffiths 1969), and cheetahs (Caro 1994). In sum, learning is a precondition allowing the occupation of many niches, and it determines key ecological interactions such as competition and predation.

2.6.2. LIFE HISTORY OF LEARNING

Life history research has focused on the effects of three physical factors—growth, effort, and senescence—on reproductive success (Stearns 1992; Roff 2002). The effects of learning have been noted, especially in a few long-term avian studies (Nol and Smith 1987; Wooler et al. 1990; Black and Owen 1995; Rattiste 2004), but the relative contribution of learning to performance throughout the life span has not been examined closely. In animals that reach final growth before sexual maturity, the three major contributors to reproductive success are effort, physiology, and learning. Reproductive effort is defined as investment in current reproduction that decreases future reproduction or survival. Although it is commonly asserted that effort should increase with age, theoretical analyses emphasize that effort could also decrease or plateau with age (Fagen 1972; Charlesworth and Leon 1976; Taylor 1991; Roff 2002). The empirical data are mixed, with some studies suggesting increased effort with age (Pugesek 1981; Clutton-Brock 1984; Candolin 1998; Poizat et al. 1999) and others documenting no change with age (W. Reid 1988).

Major physiological attributes such as muscle power and endurance increase early in the life of some species. From sexual maturity onward, physiology is subjected to senescence, defined as a decrease in body condition, associated with decreased fertility and survival rates, with increased age (Rose 1991; Kirkwood and Austad 2000). As with reproductive effort, however, theory and data indicate that patterns of senescence can diverge from the classical pattern of exponential increase in mortality rates with age (Abrams 1993; Reznick et al. 2004; Williams et al. 2006). Overall, we know relatively little about lifetime patterns of physiological performance in nonhuman animals in the wild.

Learning is somewhat similar to physical growth. Hence, the investment in learning may be highest before animals reach sexual maturity. Unlike physical growth, however, some tasks can be learned only by performing them, a feature referred to as “learning by doing” in the economic literature (Arrow 1962). Consequently, learning may contribute to a gradual increase in performance throughout an individual’s life as long as it is not impaired by senescence (Dukas 2008d).

The lifetime pattern of performance in forager honeybees is remarkably similar to that of many other species, including humans: performance is quite low initially, gradually increases to a peak at about midlife, followed by a steady decrease into old age (reviewed in Dukas 1998c, 2008d; Helton 2008). To estimate the contribution of learning to the observed increase in performance, I quantified the foraging success of bees collecting nectar from an artificial feeder placed 400 meters from the hive and bees foraging on wild flowers in a natural forest. Unlike the natural settings, which require learning a wide range of tasks, nectar collection from the artificial feeder requires little learning. Indeed, feeder bees exhibited no significant change in the net rate of nectar collection from the feeder, whereas natural foragers showed a fourfold increase in the net rate of food delivery to the colony over their first few days as foragers (fig. 2.6). The major contributors to that increase were decreases in departure weights and increases in arrival weights of foragers with experience (Dukas 2008c, 2008d).

Whereas learning seems to be the major contributor to the observed increase in performance with bee experience, physiological analyses revealed that most of the flight muscle enzymes were at their peak before bees started foraging. Proteomic analyses, however, suggested that structural changes in bees' flight muscles could translate into some increase in performance with flight experience, but this possibility has not been tested (Schippers et al. 2006). Similarly, in the feeder study just mentioned, there may have been a small, significant increase in effort with forager experience (Dukas 2008d). Overall though, the data indicate a dominant contribution of learning to forager performance with experience and minor, though perhaps significant, roles

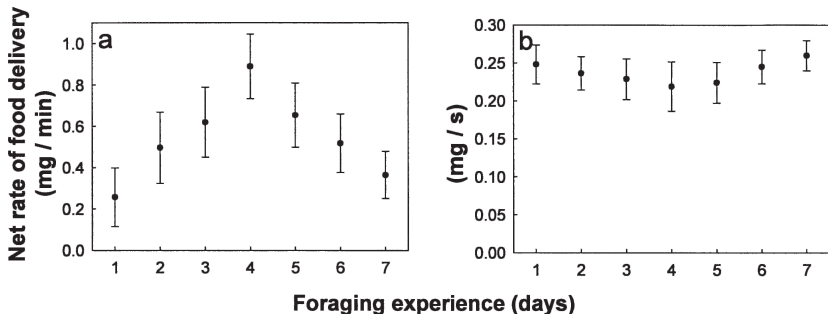


FIGURE 2.6. The net (\pm SE) rate of food delivery as a function of experience in honeybees foraging (a) in a natural forest (in mg/min) and (b) at a feeder providing 2.5 M sugar water (in mg/s). Bees in the challenging natural settings exhibited gradual improvement in performance, most likely owing to learning, but not at the trivial feeder. Data from Dukas 2008c, 2008d.

of physiological improvements and effort. This conclusion may be relevant for numerous species in which continuous learning over a large proportion of individuals' lives can translate into substantial increases in performance. In the human literature, such a cumulative effect of learning is referred to as expertise (reviewed in Ericsson et al. 2006).

2.6.3. EVOLUTIONARY SIGNIFICANCE OF LEARNING

Learning has contributed to evolutionary change in at least two major ways. First, learning can help animals cope with environmental change. That is, populations of animals that learn to survive and reproduce despite a dramatic ecological change can have the opportunity to adapt to the new environment over generations. Learning, however, can also decrease the rate of evolutionary change if individuals can maximize fitness by adjusting behaviorally to new environments such that no genetic change follows (reviewed in B. Robinson and Dukas 1999; Huey et al. 2003; Price et al. 2003). At least in birds, an aspect of learning ability, feeding innovation (Sol, chapter 7 in this volume), seems to have influenced evolutionary change. Feeding innovation in birds is positively correlated with (*i*) the number of species per taxon (Nicolakakis et al. 2003), (*ii*) the number of subspecies per species (Sol et al. 2005c), (*iii*) invasion success (Sol et al. 2002), and (*iv*) survival in novel environments (Sol et al. 2005a). The limited data for mammals, however, show no evidence that enhanced cognitive abilities increased the rate of morphological evolution in either great apes or hominoids (M. Lynch and Arnold 1988).

Second, the other major way in which learning has influenced evolutionary change is through its effect on assortative mating that contributes to reproductive isolation and speciation. In species in which mate choice is based on innate rules rather than learning, selection would act against divergence in secondary traits used for mate choice because novel traits would typically confer lower fitness. Such interference would not occur if divergence in secondary traits, such as color pattern, song, and odor, is accompanied by young learning to prefer the novel traits (Price 2008). This effect of learning is best documented in birds, in which young indeed learn from their parents and perhaps neighboring conspecifics about some of the desired characteristics of future mates (Lorenz 1970; ten Cate and Vos 1999). For example, males of the two allopatric subspecies of the zebra finch, *Taeniopygia guttata guttata* and *Taeniopygia guttata castanotis*, which reside in Indonesia and Australia respectively, differ in their plumage and song. When nestlings of both sexes were cross-fostered to the other subspecies, they all preferred to breed with the foster parents' subspecies, forming 100% hybrid pairs (reviewed in Clayton 1990).

The positive effects of learning on assortative mating may be largest in species with biparental care, in which young of either sex can learn from their parents about the desired characteristics of future mates. Learning, however, can promote assortative mating also in species with either uniparental care or no care at all. In mallards (*Anas platyrhynchos*), only the mother cares for her chicks. The young males learn the female-specific characteristics and, after sexual maturity, seek similar females. The females appear to mate with the males that court them most (Kruijt et al. 1982). It is likely, however, that the females also rely on innate mate choice mechanisms. In parasitic brown-headed cowbirds (*Molothrus ater*), young birds join conspecific birds probably based on innate cues. Both sexes learn population-specific courtship behavior from adults, and the males also perfect their courtship behavior based on feedback from the females (West and King 1988; Freeberg 1998; Freeberg et al. 2002).

Both male and female fruit flies (*D. melanogaster*) learn in the context of mate choice (section 2.5), and such learning could promote assortative mating (Dukas 2004b). To examine the effects of learning on assortative mating, I studied the closely related species pair *D. persimilis* and *D. pseudoobscura*, which have been widely used in research on speciation. These two species, which are sympatric along the Pacific West Coast, are visually indistinguishable but differ in their pheromonal composition and parameters of the male courtship song. Males of the two species indiscriminately court inter- and intraspecific females, but the females exhibit partial preference to intraspecific males. Hybridization is rare in the field but frequent in the laboratory, especially between male *D. persimilis* and female *D. pseudoobscura*. The hybrid daughters are fertile but hybrid sons are infertile (e.g., Mayr 1946; Noor 1995; Machado et al. 2002; Ortiz-Barrientos et al. 2004). Interspecific courting and mating are costly for both females and males. Females that mate interspecifically produce only half as many fertile offspring, and males waste time and energy courting interspecific females, which often reject them. Hence, learning in the context of sexual behavior could be adaptive for both females and males if it can lead to reduced interspecific matings and courting respectively.

In a series of experiments, I found that female *D. pseudoobscura* that had long-term experience with conspecific males were significantly less likely to mate with male *D. persimilis* than inexperienced females were. Males of both species that engaged in courtship and subsequent rejection by heterospecific females exhibited significantly lower levels of interspecific courtship than inexperienced males did. Furthermore, the reduced courtship was also associated with fewer interspecific matings by experienced male *D. persimilis* than by naive *D. persimilis* (fig. 2.7). Overall, it seems that the innate partial female preference for intraspecific males is increased with female experience. Males'

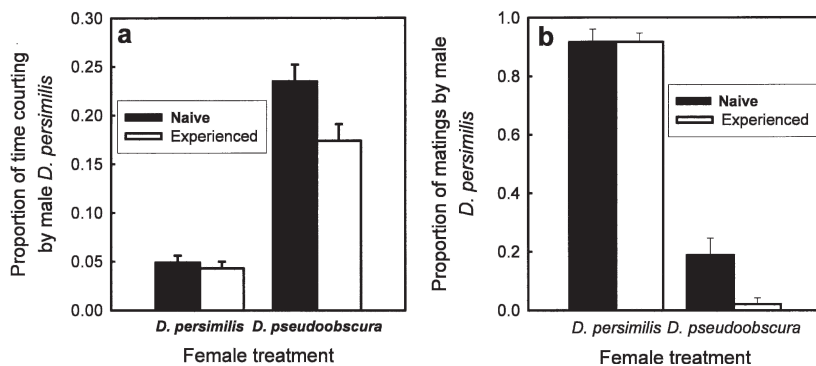


FIGURE 2.7. a. The proportion of time either naive male *D. persimilis* (black bars) or *D. persimilis* males experienced at courting female *D. pseudoobscura* (white bars) spent courting either two female *D. persimilis* or two female *D. pseudoobscura*. Each bar depicts the mean ± 1 SE for 48 males, with a total of 192 males. b. The proportion of matings in vials containing either naive male *D. persimilis* (black bars) or *D. persimilis* males experienced at courting female *D. pseudoobscura* (white bars). Each bar represents the mean ± 1 SE proportion of matings in each of 8 replicates of 24 vials each, with a total of 192 males. Data from Dukas 2008b.

responses to rejection by interspecific females amplify the female selectivity and further increase the levels of assortative mating. Hence, learning in the context of mate choice and courtship could contribute to increased levels of assortative mating that leads to speciation (Dukas 2008b, 2009).

Effects of learning on assortative mating have also been documented in fish (Magurran and Ramnarine 2004; Verzijden and ten Cate 2007) and spiders (Hebets 2003). Given the broad taxonomic distribution of the above studies and the theory indicating learning's potential importance in incipient speciation (Lachlan and Servedio 2004; Beltman et al. 2004; Beltman and Metz 2005; Price 2008), further empirical studies on this topic are needed.

2.7. Prospects

We understand better than ever some basic properties of learning and memory but learning is still not well integrated within ecology and evolution. Perhaps the most fundamental unanswered question concerns the evolution of learning. Do all animals with nervous systems learn (section 2.3.2)? Can we identify specific cellular mechanisms associated with the evolution of learning? Have physiological costs of learning and memory played a crucial role in shaping the evolution of learning (section 2.4.2)? There have been thus far only rudimentary explorations of such questions (e.g., W. Wright et al. 1996). Increased understanding of the neurogenetic mechanisms underlying

learning and memory has led to the realization that there is great similarity in these mechanisms across all animals. This means that neurogenetic tools developed for one model species may be employed for addressing evolutionary ecological questions regarding learning in other species as well (Fitzpatrick et al. 2005; Smid et al. 2007).

Learning is a key factor in the life history of most animals (section 2.6.2), yet it has not been well integrated into the life history literature, which has focused on physical traits such as growth, effort, and senescence (e.g., Stearns 1992). There are a few well-studied subdisciplines, including spatial memory (chapter 6 in this volume), song learning (chapters 4 and 5 in this volume), and social learning (chapter 13 in this volume) and a variety of other studies relating behavior or ecology to brain-region size (chapter 7 in this volume; Clutton-Brock and Harvey 1980; Healy and Guilford 1990; Barton et al. 1995). But we still do not possess a coherent view of the life history trade-offs determining relative investments in learning and memory among animals.

Finally, recent work on mechanisms of speciation makes it clear that learning can play an important role in population divergence (Price 2008). Despite the traditional focus on birds in work on learning and speciation, learning may be as important in other taxa, including the most commonly used model system for speciation, fruit flies *Drosophila* spp. (section 2.6.3). We especially need a large body of empirical work that examines the role of learning in speciation in particular and evolutionary change in general. As usual, evaluating what we already know helps us choose what to learn next.

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