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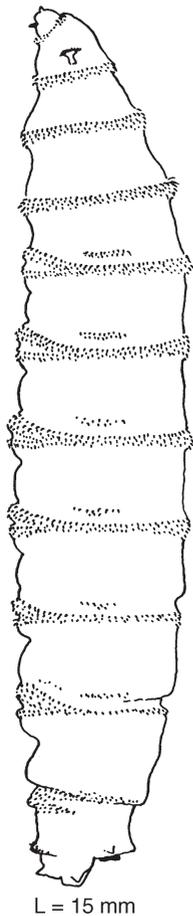


FIGURE 5 A legless, peg-shaped maggot of the higher flies. (Reproduced from A. Peterson, 1951, *Larvae of Insects*, Vol. 2, with permission of Jon A. Peterson.)

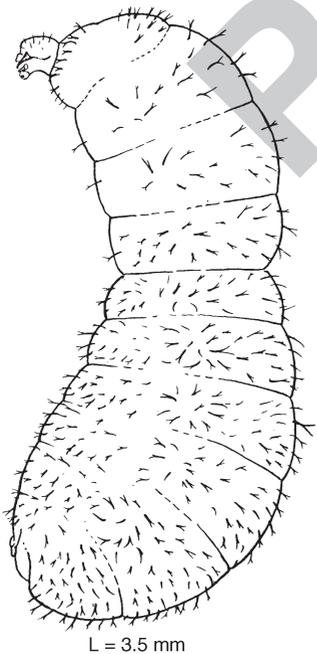


FIGURE 6 A baglike ant larva. It and other similar larvae are commonly called "grubs." (Reproduced from A. Peterson, 1951 *Larvae of Insects*, Vol. 2, with permission of Jon A. Peterson.)

Learning

Daniel R. Papaj
University of Arizona

A butterfly learns to search for the shape of its preferred host plant's leaves and, contemporaneously, for the color of preferred nectar sources. A parasitoid wasp learns color, pattern, and odor components of its insect host's microhabitat. A grasshopper avoids feeding on a plant associated with a recent digestive malaise. An emerging adult paper wasp imprints on odor cues in its nest, using the odors to distinguish nestmates from nonnestmates. A male damselfly learns to recognize andromorphs (male-mimicking females) as females. A fly improves its depth perception with experience. A bee memorizes a sequence of visual landmarks between its nest and a patch of flowers, as well as the distance between landmarks. All of these are examples of learning, a phenomenon that is ubiquitous throughout the animal kingdom and, as these examples illustrate, well represented within insects. In fact, learning has been documented in all major insect orders. While best studied in the context of foraging for food or oviposition sites, evidence of learning has also been obtained in relation to water consumption, mate finding and choice, territoriality, predator avoidance, dispersal, migration, kin recognition, and thermoregulation.

LEARNING CHARACTERIZED

Characteristics

Learning eludes an easy, satisfying definition, but the following characteristics constitute a useful guide. Learning involves an enduring change in behavior with experience, the change usually progressing gradually with continued experience to some asymptote. Learned behavior is often modified by novel experiences, and effects of experience eventually wane if not reinforced.

Associative vs Nonassociative Learning

Learning can be categorized as nonassociative or associative. Nonassociative learning includes habituation and sensitization. Habituation involves the waning of a response to a stimulus upon repeated presentation of that stimulus. Alternately, repeated presentation of a stimulus sometimes enhances a response to that stimulus and often to related stimuli, a process termed sensitization. Associative learning involves pairing a stimulus with another stimulus, or with a motor pattern, such that the response to the first stimulus is altered as a consequence of the pairing. Associative learning is typically evaluated in two kinds of paradigms: classical (Pavlovian) conditioning and instrumental conditioning.

Classical and Instrumental Conditioning

In classical conditioning, an unconditioned stimulus (US) that elicits an unconditioned response is paired in time and space with a novel stimulus, the conditioned stimulus (CS). As a consequence of the pairing, the CS subsequently elicits a conditioned response. Both appetitive and aversive forms of classical conditioning have been documented in insects. Most of what we know about classical conditioning in insects has involved classical conditioning of the proboscis extension reflex (PER), principally in honey bees.

A case for associative learning is strengthened by evidence of discrimination learning. Discrimination learning (sometimes called differential conditioning) controls for effects of sensitization to a CS by training to two CSs, one which is reinforced with a reward (CS+) and one which is not (CS-). If learning is associative, response to the CS+ only is heightened, relative to controls. Discrimination learning is well documented in bees, hymenopterous parasitoids, moths, butterflies, cockroaches, and fruit flies. A case for associative learning is similarly supported if learning is restricted to forward pairing. In forward pairing, the CS is presented shortly before the US, whereas, in backward pairing, the CS is presented shortly after the US. Insects, like vertebrates, show strong learning in forward-pairing regimes but little or no learning in backward-pairing or random-pairing regimes.

In instrumental conditioning (roughly equivalent to operant conditioning), presentation of a reinforcing stimulus is contingent upon the insect's own motor actions. For example, an entirely novel motor pattern can be generated through a process of trial and error, as when a bee or butterfly learns how to extract nectar from a flower. A standard operant conditioning paradigm in the laboratory requires a tethered orthopteran to move its leg in response to an electric shock, heat, or access to food. A headless roach learns such a task, demonstrating that conditioning can occur at the level of ganglia.

Learning a given task in nature probably involves a combination of stimulus-stimulus and stimulus-response associations. When an insect pollinator learns nectar-extraction routines for different flowers, for example, it simultaneously learns identifying features of each type of flower, allowing the appropriate motor routine to be expressed on the appropriate flower.

Miscellaneous Types

Various forms of associative learning beyond the basic types have special meaning to students of learning. Food aversion learning, strongly implicated in work on vespine wasps, grasshoppers, mantids, and caterpillars, involves avoidance of food stimuli associated with a digestive malaise. Food aversion learning is noteworthy because an aversion can form even when a long period of time (hours) passes between ingestion of a food and the resulting illness.

Spatial learning is an important component of insect navigation. Commonly traversed routes are learned during homing by ants, bees, and wasps, and traplining is learned by bees and butterflies. Honey bees may additionally possess a topographically organized landscape memory that allows them to navigate along a novel route. Spatial learning is useful in contexts other than movement of the whole organism; for instance, bees learn to discriminate textures with their antennae and use such learning to evaluate the microtexture of flower petals.

One form of learning of significance in vertebrates which has not been documented to date in insects is observational learning, in which a subject imitates the motor actions of a demonstrator. Nevertheless, social interactions do influence what insects learn. Honey bees and bumble bees, for example, evaluate floral scents borne by returning foragers and forage selectively for those scents.

LEARNING PROCESSES

Many associative learning processes that have been described for vertebrates have also been shown in insects. The following list of selected processes is derived mainly from work on honey bees, unless otherwise noted.

Generalization refers to an animal's tendency to respond to stimuli that were not reinforced but that are related to a reinforced stimulus (A+) along some perceptual dimension. Moths and honey bees have been shown to generalize odors according to similarities in functional groups and carbon-chain length.

Blocking occurs when an animal that first learns to respond to a stimulus (A+), and is then reinforced on A and a novel stimulus, B, presented together ([AB]+), subsequently fails to show a heightened response to B alone, relative to controls. Learning of stimulus B has been blocked by coupling with the previously learned stimulus A. Blocking illustrates that temporal pairing between a CS and a US is not sufficient for associative learning to take place; rather, a new CS must convey new information in order to be learned. Whereas blocking is a robust phenomenon in vertebrates, studies of blocking in bees and fruit flies have yielded mixed results. Where blocking has been demonstrated, it seems to be restricted to intramodal stimuli (e.g., odor blocking in honey bees).

Overshadowing occurs when an animal reinforced on a compound of stimuli A and B ([AB]+) shows little response to B alone, relative to when reinforced on B alone (B+). As with blocking, overshadowing illustrates that temporal pairing between a CS and a US is not sufficient for associative learning to take place.

Sensory preconditioning occurs when an insect presented simultaneously with two stimuli in the absence of reinforcement ([AB]-), then reinforced on one stimulus (A+), subsequently shows a heightened response not only to A but also to B. During exposure to [AB], the insect learns that A

626 Learning

and B belong together. Observed in *Drosophila* fruit flies and honey bees, sensory preconditioning illustrates that a stimulus does not have to be paired directly with a US in order for an association between the stimulus and the US to form.

Second-order conditioning refers to the capacity for a stimulus, once conditioned, to serve as a US in the conditioning of another stimulus. Second-order conditioning may play a major role in learning complex mixtures of stimuli, such as odor blends.

Patterning is evaluated by reinforcing two stimuli in turn (A+, then B+) and then explicitly not reinforcing a compound of those stimuli ([AB]−). Under this protocol, PER odor conditioning in bees shows “negative patterning,” responses being greater to individual odors than to the compound. This result can be explained only if the insect treats the compound [AB] as a unit and relates it to the absence of reinforcement. Such learning is referred to as configural learning.

Rule extraction has been demonstrated with the use of delayed matching-to-sample tasks in which honey bees are required to respond to a stimulus that matches a sample stimulus recently experienced. Bees not only solve the task but also transfer the matching to stimuli not previously reinforced. For example, bees trained to match a color can subsequently match patterns of lines and, remarkably, bees trained to match an odor can subsequently match colors too. Such results have been interpreted to mean that insects can form a concept of “sameness.” When trained in a delayed non-matching-to-sample task in which they must choose the stimulus that does not match the sample, bees again perform well and make similar transfers, showing a grasp of a “difference” relation. Bees also learn to extract bilateral symmetry from a series of rewarded patterns and subsequently transfer that extraction to evaluation of novel patterns.

MEMORY

Associative memory in insects, as in vertebrates and other animals, is time-dependent and phasic. Recent work on fruit flies and honey bees suggests as many as five memory phases: (1) an early and (2) a late form of short-term memory [eSTM and lSTM], (3) a midterm memory [MTM], and two forms of long-term memory (in honey bees, characterized as (4) an early form [eLTM] and (5) a late form [lLTM]; in *Drosophila*, characterized as (4) an anesthetic-resistant form and (5) a parallel, susceptible form. STM forms immediately upon association, is short-lived (seconds to minutes), and is relatively easily erased by conflicting information or treatment by cooling or shock. eSTM is characterized by a relatively nonspecific appetitive arousal and is highly susceptible to interference by new, conflicting information or by cooling. lSTM is more stable, is more specific, and takes longer to form than eSTM. The transition from STM to MTM after a single learning trial requires several minutes. MTM is more resistant to interference than STM, requiring hours to decay.

LTM takes longer still to form than either STM or MTM, involves longer lasting changes (hours to weeks), and is relatively resistant to interference. In bees, formation of LTM requires multiple learning trials. LTM is highly context-specific; landmarks learned by bees around their feeder, for example, may be entirely ignored when presented at a novel location. eLTM and lLTM have been distinguished in terms of the effects of inhibiting protein synthesis: synthesis inhibition after 24 h degrades memory, whereas inhibition after 3 days does not. Effects of inhibition depend on the time between learning trials, with closely spaced trials (termed “massed trials”) resulting in memory that is independent of protein synthesis.

The underlying processes involved in memory formation are beginning to be revealed. In honey bees, a “value” neuron, the VUM_{mx1} of the subesophageal ganglion, which fires in response to sucrose stimulation, is proposed to be part of the US pathway. In PER odor conditioning studies, artificial depolarization of the VUM_{mx1} neuron just following presentation of an odor generates a conditioned response to the odor. The VUM_{mx1} neuron, which uses octopamine as a neurotransmitter, converges on two brain neuropils, the antennal lobe and the mushroom bodies. Consistent with these observations, olfactory memories can be established by odor-coupled injection of octopamine into either the antennal lobe or the mushroom bodies. The pattern of octopamine effects suggests that antennal lobe processes may relate more to eSTM, whereas mushroom body processes may relate more to lSTM and LTM.

To what degree these findings pertain only to honey bees or only to odor learning is uncertain. Analysis of *Drosophila* mutants suggests that the mushroom bodies are important for odor learning but dispensable for visual or tactile learning. Studies of locusts have indicated effects of feeding experience on diet choice that resemble discrimination learning, but are based on an entirely novel mechanism. This taste-feedback mechanism involves adjustments in the level of sensitivity to nutrients in the hemolymph.

FUNCTION OF LEARNING

In a sense, the function of associative learning is obvious. Animals learn by association to orient toward stimuli predicting positively rewarding resources (such as sugar, pollen, food plant, hosts) and away from stimuli predicting negatively rewarding events (shock, heat, toxins, predators). Likewise, habituation is a means for reducing energy-wasteful, time-consuming responses to meaningless stimuli. In either case, however, learning is needed only if the appropriate responses cannot be predicted without benefit of experience, else an insect could respond (or not respond) innately. Even in an unpredictable environment, whether learning yields higher fitness than innate behavior depends on the relative costs of learning. A robust assessment of costs and benefits of learning has proved elusive, perhaps in part because individual fitness in nature is especially difficult to measure in *Drosophila* and

honey bees, the systems in which learning processes and mechanisms have been best studied.

ADAPTATION, CONSTRAINT, AND LEARNING

Limits to Learning and Memory

Of interest to behavioral ecologists is the degree to which learned behavior reflects adaptation by natural selection versus constraints on selection. Generalization (see above), for example, may seem at first to reflect a constraint on learning, but conceivably represents an adaptive mechanism of imprecision. A pollinator, for example, that responded only to the precise odor blend emitted by the first rewarding flower encountered might never visit another flower, owing to among-flower variation in the blend.

A classic case study of limits on learning and memory in nature that interested Darwin himself concerns the tendency for bees, butterflies, and other pollinators to show greater fidelity to one or a few floral species than expected based on the profitabilities of those species. According to one point of view, this so-called floral constancy is dictated by limits on the acquisition, retention, and/or retrieval of stored information about the floral resource.

That foraging success in insects is limited in terms of acquisition and retention seems unlikely at the level of LTM. LTM in insects, as mentioned above, is extraordinarily durable and the amount of information that can be maintained in LTM, as currently understood, is extremely impressive. Butterflies can learn visual cues in two foraging modes (nectar collection and oviposition) simultaneously, showing meaningful responses in each instance in just a single trial. Bees can be trained to distinguish multiple rewarded stimuli from multiple unrewarded ones and to link features of eight or more different flower species to the time of day at which nectar is available. These features include flower color, odor, pattern, and microtexture. In addition, a bee learns the location, profitability, and visual landscape associated with a rewarding patch of flowers, as well as the route between hive and patch and, in conjunction with the sun compass used to navigate, even the pattern of movement of the sun through the sky.

Retention at the level of LTM is similarly impressive. Bees have been shown to retain LTM without reinforcement for several weeks, a period of time comparable to average worker life expectancy. In *Tribolium* beetles and *Drosophila*, there is evidence that memory formed in the larval stage persists through metamorphosis.

If pollinators are limited at all in memory, it may be at the level of STM. As noted above, STM is particularly vulnerable to conflicting information; this fact may make it difficult for a bee once fixed on a flower type to switch to a novel one. Alternatively, the key to floral constancy may lie in the retrieval of stored information, specifically a constraint on the minimum time required to activate information stored in

LTM and a limited capacity to activate multiple memories at once (together, limits on what for vertebrates has been referred to as working memory).

Learning and Memory as Products of Adaptation

An alternative, albeit not mutually exclusive, view holds that natural selection generates an adaptive balance between activation and suppression of memory, tuning that balance finely to the specific ecological requirements of a given species. For example, floral constancy might conceivably permit workers in a colony to partition floral resources efficiently, in which case the properties of learning and memory that contribute to constancy would be viewed as adaptive. It has even been proposed that memory dynamics in bees are tightly matched to foraging activity rhythms as well as the spatial patterning of the floral resource.

Abundant propositions as to adaptive specialization in learning have been made, especially from a comparative standpoint: "Insects of a given species should be prepared to learn particularly well those stimuli relevant to that species' needs." "Social insects should learn better than solitary ones (owing to the demands of a complex and unpredictable social environment)." "Generalist insects should learn better than specialists." For none of these propositions is there compelling evidence, nor will there be until better descriptions are made of learning in an ecological context, learning protocols are brought closer in rigor to those employed in comparative psychology, and more insect species are evaluated.

For now, the primary comparison to be made is a comparison between learning in insects and in vertebrates. Here, the pattern is one of shared features. Despite significant phylogenetic distance between insects and vertebrates, and despite substantial differences in their underlying physiology, there is a remarkable congruence in the diversity and form of learning processes in these taxa (see above). The similarities may reflect shared ancestry, evolutionary convergence, or both. A finding of evolutionary convergence would imply that certain universal, yet to be clearly defined functional principles govern the evolution of learning and memory processes.

See Also the Following Articles

Brain • Dance Language • Neuropeptides

Further Reading

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Legs

Peter H. Adler

Clemson University

One of the most generally known and oft-repeated facts about insects is that they possess three pairs of legs, one pair each on the prothorax, mesothorax, and metathorax. Indeed, this condition is in the fundamental ground plan of insects and is amply represented in the fossil record. The condition inspired Latreille's taxon Hexapoda (Greek *hexa*, six, and *poda*, foot). Exceptions to the hexapodous condition are found in the apodous, or legless, insects that have secondarily lost their legs, typically as a result of selection for an obligatory parasitic or sedentary existence.

The six-legged condition is derived from an ancestral arrangement in which legs occurred on the majority of body segments. Over evolutionary time, the serially uniform legs became modified in the insectan lineage into the characteristic mouthparts, thoracic legs, and various abdominal appendages, such as cerci and genitalia, while typically becoming lost on other abdominal segments. Further evolution of the basic six-legged condition in the insectan lineage has resulted in an enormous diversity of structure and function. This structural and functional diversity of legs, along with the acquisition of wings without the loss of legs, which is a condition unique to insects, undoubtedly has been a key factor in the numerical success of insects and their representation in nearly every habitat on the planet. The exquisite diversity in leg structure plays an important role in the taxonomy and classification of insects.

STRUCTURE

In the classic textbook interpretation, the insectan leg has six well-sclerotized segments, arranged proximal to distal: the coxa, trochanter, femur, tibia, tarsus, and pretarsus. A more fundamental and complete segmentation scheme, which facilitates the recognition of leg and leg-derived homologies among all arthropods, involves 10 or 11 segments. These segments include the epicoxa (debatably present as the wing articulation and a fused portion of the tergum), subcoxa (absorbed into the pleuron), coxa, trochanter, prefemur

(typically fused with the trochanter), femur, patella (fused with the tibia), tibia, basitarsus, eutarsus (often subdivided), and pretarsus. A more modern interpretation of the free leg of extant insects, therefore, depicts it as consisting of seven to eight distinct segments, which are the classical six plus a basitarsus and a prefemur, in some insects.

Each segment in the insectan leg, unless secondarily lost or fused, is independently movable by muscles inserted on its base. Thus, subdivisions of the eutarsus, marked by flexible cuticle but without corresponding internal muscles, are not true segments; these subdivisions are referred to as tarsomeres. The areas of flexion between segments are joints, and the well-sclerotized contact points in the joints are the condyles. The various joints contribute to the mechanical efficiency of the leg. The articulation between the coxa and the body, for example, allows the leg to move forward and rearward, whereas that between the coxa and the trochanter allows the leg to be lifted at the end of the backstroke and depressed at the beginning of the backstroke.

Leg joints are of two types. Monocondylic joints have a single point of articulation, somewhat like a ball-and-socket joint, and usually are situated dorsally. They allow considerable freedom of movement and are characteristic of the legs of larval insects. Dicondylic joints consist of an anterior and a posterior condyle, or a dorsal and ventral condyle in the case of the trochanterofemoral joint. They typically limit movement to that of a hinge. Adult legs usually have dicondylic joints, although the tibiotarsal joint is often monocondylic.

The coxa (plural coxae) is typically short and rather stout, although it varies in shape among taxa. It is set in a coxal cavity and articulates with the thorax at the coxal process of the pleural sulcus (groove). Quite often, it also articulates with the thoracic trochantin and sternum, somewhat restricting its movement. To withstand the forces of movement, the coxa is strengthened by a ringlike basicostal sulcus that sets off a basal sclerite, the basicoxite. Internally, the basicostal sulcus is expressed as a ridge, the basicosta, that provides for muscle attachment. Posterior to the point of articulation, the basicoxite is called the meron and in insects such as adult Neuroptera and Lepidoptera, it can be quite large. In higher Diptera, the meron is detached from the coxa and forms a plate in the mesothoracic pleuron. In some insects, an additional external groove, the coxal sulcus, divides the coxa lengthwise.

The trochanter is small and freely movable in a vertical direction on the coxa, but it is often rather fixed to the base of the femur. In the larvae and adults of numerous fossil insects and a few extant taxa, such as Odonata, two trochanteral segments are present, the distal one being the prefemur.

The femur (plural femora) is usually the largest and strongest segment of the leg. Its size is related to the mass of the tibial extensor muscles within it, varying from a small, thick segment in larval insects to the enormous segment in the hind leg of jumping Orthoptera. The femur often is