



Invertebrate learning and cognition: relating phenomena to neural substrate

Clint J Perry, Andrew B Barron and Ken Cheng*

Diverse invertebrate species have been used for studies of learning and comparative cognition. Although we have gained invaluable information from this, in this study we argue that our approach to comparative learning research is rather deficient. Generally invertebrate learning research has focused mainly on arthropods, and most of that within the Hymenoptera and Diptera. Any true comparative analysis of the distribution of comparative cognitive abilities across phyla is hampered by this bias, and more fundamentally by a reporting bias toward positive results. To understand the limits of learning and cognition for a species, knowing what animals cannot do is at least as important as reporting what they can. Finally, much more effort needs to be focused on the neurobiological analysis of different types of learning to truly understand the differences and similarities of learning types. In this review, we first give a brief overview of the various forms of learning in invertebrates. We also suggest areas where further study is needed for a more comparative understanding of learning. Finally, using what is known of learning in honeybees and the well-studied honeybee brain, we present a model of how various complex forms of learning may be accounted for with the same neural circuitry required for so-called simple learning types. At the neurobiological level, different learning phenomena are unlikely to be independent, and without considering this it is very difficult to correctly interpret the phylogenetic distribution of learning and cognitive abilities. © 2013 John Wiley & Sons, Ltd.

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INTRODUCTION

While there is still no universally accepted definition of learning, most important aspects of learning are captured in the following definition by Domjan (Table 1, Ref 181). Learning is an enduring change in the mechanisms of behavior involving specific stimuli and/or responses that results from prior experience with those or similar stimuli and responses. Cognition is an even more problematic term. While there is no consensus definition for cognition, the term is most often applied to the subset of learning phenomena that somehow involve more than basic associative processes.¹⁸³

Most research on learning has been performed with vertebrate species. Over the past several decades, however, invertebrate models have become key in propelling the study of the mechanisms of learning. They make effective, inexpensive, and arguably more ethical study subjects, for which experimental conditions are more easily controlled. They have generally smaller nervous systems than vertebrates, but yet exhibit a broad repertoire of behavior and learning abilities. The range of learning abilities explored and documented in invertebrates spans from the simplest non-associative forms (habituation and sensitization) to well-known associative learning (both classical and instrumental), to other forms of learning variously described as more cognitive, complex, or specialized, such as number-based learning and relational learning.¹⁸³

*Correspondence to: Ken.Cheng@mq.edu.au

Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

TABLE 1 | Examples of Various Types of Learning Across Invertebrate Phyla. The Footnotes in the Table Also Refer to Reference Numbers 1–181.

	Triploblastic														
	Deuterostomes							Protostomes							
	Metazoa							Arthropods							
	Chordates	Echinoderms	Insects	Crustaceans	Arachnids	Merostomata	Myriapods	Maxillipods	Cephalopod Molluscs	Nematodes	Annelids	Gastropod Molluscs	Platyhelminthes	Rotifers	Cnidarians
Habituation	Sea squirt ¹ Sea urchin ^{2,3} Sea cucumber ⁴	Honeybee ⁵ Bumblebee ¹⁵ Wasp ⁹	Cockroach ^{6,7} Cricket ¹⁶ Locust ^{20,21}	Drosophila ^{8,11} Blowfly ¹⁷	Ant ¹⁴ Hawkmoth ¹⁸	Crab ^{2,24} Crayfish ^{25,26} Lobster ²⁷	Spider ²⁸	Horseshoe crab ²⁹ Millipede ³⁰ Barnacle ^{31,32}	Octopus ³³ Squid ³⁴	<i>C. elegans</i> ^{35,36}	Leech ^{37,39} Earthworm ^{40,42} Polychaetes ^{43,44}	Sea slug ^{45,47} Pond snail ⁴⁸ Chiton ⁴⁹ Clam ⁵⁰ Land snail ⁵¹	Flatworm ^{52,53}	Planolida ⁵⁴	Jellyfish ⁵⁵ Sea anemone ^{56,59}
Sensitization	Sea squirt	Honeybee ⁶⁰ Wasp ⁶⁴	Cockroach ⁶¹	Drosophila ⁶²	Hawkmoth ⁶³	Crab ⁶⁵ Crayfish ⁶⁶			Squid ⁶⁷	<i>C. elegans</i> ⁶⁸	Leech ⁶⁹ Earthworm ⁷⁰ Polychaetes ⁷¹	Sea slug ^{72,74} Pond snail ⁷³	Flatworm ⁷⁶		
Classical conditioning	Starfish ⁷⁷	Honeybee ^{78,80} Bumblebee ⁸⁵ Locust ⁸⁶	Cockroach ⁸¹ Cricket ⁸² Wasp ⁸³	Drosophila ⁸⁴ Blowfly ⁸⁷ Butterfly ⁸⁹	Ant ^{84,84} Hawkmoth ⁸⁸	Crab ^{89,91} Crayfish ⁹⁴ Lobster ⁹⁵	Spider ^{96,97} Whip spider ⁹⁸	Horseshoe crab ⁹⁹	Octopus ¹⁰⁰ Cuttlefish ¹⁰¹	<i>C. elegans</i> ^{102,103}	Leech ^{104,105} Earthworm ¹⁰⁶	Sea slug ^{107,108} Pond snail ¹⁰⁹ Land snail ¹¹⁰	Flatworm ¹¹¹		Sea anemone ¹¹²
Reversal learning		Honeybee ^{103,114} Cricket ¹¹⁵	Cockroach ¹¹⁵ Hawkmoth ¹¹⁶	Drosophila ¹¹⁶ Locust ¹¹⁹	Ant ¹¹⁷ Butterfly ¹²⁰	Crab ¹²¹ Crayfish ¹²² Lobster ¹²³			Octopus ¹²⁴ Cuttlefish ¹²⁵	Earthworm ¹²⁶					
Latent inhibition		Honeybee ^{103,117,119}								<i>C. elegans</i> ¹³⁰	Leech ¹⁰⁵				
Peak shift		Honeybee ^{131,133}	Bumblebee ¹³⁴	Hawkmoth ¹³⁵											
Operant conditioning		Honeybee ¹³⁶ Bumblebee ¹⁴⁰ Locust ¹⁴⁷	Cockroach ¹³⁷ Cricket ¹⁴⁴	Drosophila ^{138,140} Blowfly ¹⁴³	Ant ^{141,142} Hawkmoth ¹⁴⁶	Crab ^{148,149} Crayfish ^{150,152} Lobster ¹⁵³			Octopus ^{154,158}			Sea slug ¹⁵⁶ Pond snail ^{157,158}			
Contextual learning		Honeybee ^{159,164} Bumblebee ¹⁶⁸	Cockroach ¹⁶⁵ Cricket ¹⁶⁹	Drosophila ¹⁶⁶	Ant ¹⁶⁷	Lobster ¹⁷⁰									
Number-based learning		Honeybee ^{171,173}	Beetle ¹⁷⁴												
Navigation learning															
Concept learning															

TABLE 1 | Footnote Continued

- ¹Sea Quirt, *Ciona intestinalis*. Stimulus: light exposure or light cessation. Response: phototaxis—swimming.
- ²Sea urchin, *Arbacia punctulata*. Stimulus: light exposure. Response: phototaxis.
- ³Sea urchin, *Centrostephanus longispinus*. Stimulus: shadow. Response: spine raising.
- ⁴Sea cucumber, *Cucumaria pulcherrima*. Stimulus: touch. Response: contraction of tentacle.
- ⁵Honeybee, *Apis mellifera*. Stimulus: Sucrose applied to antennae. Response: proboscis extension.
- ⁶Cockroach, *Gromphadorhina portentosa*. Stimulus: handling by humans. Response: hissing.
- ⁷Cockroach, *Periplaneta americana*. Stimulus: air puff. Response: escape reflex—running.
- ⁸Drosophila, *Drosophila melanogaster*. Stimulus: odor. Response: startle response—running.
- ⁹Drosophila, *Drosophila melanogaster*. Stimulus: visual stimuli simulating approach—vertical stripes moving from middle of vision to lateral edges. Response: landing response—extend forelegs forward.
- ¹⁰Drosophila, *Drosophila melanogaster*. Stimulus: sugar applied to foot. Response: proboscis extension response.
- ¹¹Drosophila, *Drosophila melanogaster*. Stimulus: shock. Response: electroshock avoidance—spatially avoiding a copper grid.
- ¹²Drosophila, *Drosophila melanogaster*. Stimulus: exposure to sexually immature males. Response: courtship behavior.
- ¹³Drosophila, *Drosophila melanogaster*. Stimulus: air puff applied to thoracic bristles. Response: cleaning reflex—pattern of legs movements over area stimulated area.
- ¹⁴Ant. *Pheidole tucsonica* and *Pheidole gilvescens*. Stimulus: exposure to worker from different colony. Response: aggressive behavior—fighting.
- ¹⁵Bumblebee, *Bombus impatiens*. Stimulus: Colored and patterned artificial flowers in a maze. Response: approach behavior.
- ¹⁶Cricket, *Teleogryllus oceanicus*. Stimulus: ultrasound from a speaker. Response: startle response—rapid turn during flight.
- ¹⁷Blowfly, *Calliphora vomitoria*. Stimulus: rotation of patterned disc. Response: cardiac response—inhibition of forward beating of heart; and motor response—body movement.
- ¹⁸Hawkmoth, *Manduca sexta*. Stimulus: tactile deflection of hairs on proleg. Response: Proleg withdrawal reflex.
- ¹⁹Wasp, Hymenoptera, Pteromalidae. Stimulus: exposure to receptive and non-receptive females. Response: duration of courtship and pattern and number of patterned head movements during courtship.
- ²⁰Locust, *Schistocerca gregaria*. Stimulus: exposure to small crowd of conspecifics. Response: escape response—walking away or jumping.
- ²¹Locust, *Schistocerca gregaria*. Stimulus: feeding deterrent—nicotine hydrogen tartate. Response: avoidance of food—not feeding.
- ²²Crab, *Chasmagnathus granulatus*. Stimulus: shock. Response: escape response—running.
- ²³Crab, *Uca vomeris*. Stimulus: approaching dummy predators. Response: escape response: running.
- ²⁴Crab, *Uca annulipes*. Stimulus: approaching human. Response: escape response—running.
- ²⁵Crayfish, *Procambarus clarkii*. Stimulus: brief lateral compression of the abdomen. Response: tail-flip escape reflex.
- ²⁶Crayfish, *Procambarus clarkii*. Stimulus: bright light. Response: tail-flip escape reflex.
- ²⁷Lobster, *Panulirus argus*. Stimulus: chemical mixture—artificial crab mixture. Response: food-search response.
- ²⁸Spider, *Cyclosa conica*. Stimulus: sounding with a tuning fork. Response: escape—falling from web.
- ²⁹Horseshoe crab, *Limulus polyphemus*. Stimulus: tactile stimulation of the gills with puffs of air. Response: Muscle activity measured via chronically implanted electrodes.
- ³⁰Milipede, *Orthoporus texicolens*. Stimulus: vibration. Response: coiling.
- ³¹Barnacle, *Balanus improvisus*. Stimulus: shadow. Response: shadow reflex—withdraw of cirri and closing the opercular plates.
- ³²Barnacle, *Balanus improvisus*. Stimulus: shadow. Response: shadow reflex—withdraw of cirri and closing the opercular plates.
- ³³Octopus, *Octopus vulgaris*. Stimulus: food and non-food objects. Response: exploration.

TABLE 1 | Footnote Continued

- ³⁴Squid, *Lolliguncula brevis*. Stimulus: predator model. Response: escape jet.
- ³⁵*C. elegans*, *Caenorhabditis elegans*. Stimulus: tap (tactile). Response: withdrawal.
- ³⁶*C. elegans*, *Caenorhabditis elegans*. Stimulus: water soluble chemicals. Response: locomotion towards/away from stimulus.
- ³⁷Leech, *Helobdella stagnalis*. Stimulus: shadow. Response: ventilatory response.
- ³⁸Leech, *Hirudo medicinalis*. Stimulus: touch. Response: shortening.
- ³⁹Leech, *Hirudo medicinalis*. Stimulus: tactile—light stroking. Response: swimming response.
- ⁴⁰Earthworm, *Lumbricus terrestris*. Stimulus: shock. Response: twitching response.
- ⁴¹Earthworm, *Lumbricus terrestris*. Stimulus: air puff. Response: backward movement.
- ⁴²Earthworm, *Lumbricus terrestris*. Stimulus: light. Response: contraction response.
- ⁴³Polychaeta, *Branchiomma vesiculosum*. Stimulus: shadow. Response: withdrawal reflex.
- ⁴⁴Polychaeta, *Nereid diversicolor*. Stimulus: touch, light, shock. Response: withdrawal reflex.
- ⁴⁵Sea slug, *Aplysia californica*. Stimulus: touch. Response: gill-withdrawal.
- ⁴⁶Sea slug, *Pleurobranchaea californica*. Stimulus: light. Response: withdrawal.
- ⁴⁷Sea slug, *Tritonia diomedea*. Stimulus: chemical—NaCl. Response: escape response—swimming.
- ⁴⁸Pond snail, *Lymnaea stagnalis*. Stimulus: touch and shadow. Response: withdrawal response.
- ⁴⁹Chiton, *Chiton tuberculatus*. Stimulus: shadow. Response: retraction of tentacles.
- ⁵⁰Clam, *Mya arenaria*. Stimulus: sudden light decrease. Response: siphon withdrawal.
- ⁵¹Land Snail, *Helix albolabris*. Stimulus: jerking of substratum. Response: withdrawal of tentacles.
- ⁵²Flatworm, Stimulus: touch. Response: contraction.
- ⁵³Flatworm, Stimulus: touch. Response: convulsive movement.
- ⁵⁴Philodina, *Rotifer philodina*. Stimulus: touch. Response: body contraction.
- ⁵⁵Jellyfish, *Aurelia aurita*. Stimulus: touch. Response: protective response—contraction.
- ⁵⁶Sea anemone, *Actinia equina*. Stimulus: exposure to conspecifics. Response: aggressive behavior—inflation and attacking with tentacles.
- ⁵⁷Sea anemone, *Stolchactis helianthus*. Stimulus: water droplet. Response: body contraction.
- ⁵⁸Sea anemone, *Adamsia rondeletii*, *Bunodes gemmaceus*, *Helliactis bellis* and *Eudendrium*. Stimulus: touch. Response: body contraction.
- ⁵⁹Sea anemone, Stimulus: fish juice on paper. Response: feeding response/acceptance of paper.
- ⁶⁰Honeybees, *Apis mellifera*. Stimulus: sucrose applied to antennae and/or proboscis. Response: proboscis extension response motor program measured through electrophysiological recording of M17 muscle activity.
- ⁶¹Cockroach, *Blaber craniifer*. Stimulus: air puff onto the terminal appendices of the abdomen with body fixed and legs free. Response: escape response measured via electromyographic recording
- ⁶²Drosophila, *Drosophila melanogaster*. Stimulus: intermittent doses of cocaine. Response: multiple reflexive motor responses—e.g. intense grooming, paralysis.
- ⁶³Hawkmoth, *Manduca sexta*. Stimulus: poking or pinching of prolegs. Response: defense response—rapid bending that accurately propels the head towards the stimuli.
- ⁶⁴Wasp, *Leptopilina boulardi*. Stimulus: odor. Response: oviposition probing.
- ⁶⁵Crab, *Chasmagnathus granulatus*. Stimulus: shadow. Response: escape response—running.
- ⁶⁶Crayfish, *Procambarus clarkii*. Stimulus: shock. Response: escape response—tail flip.
- ⁶⁷Squid, *Loligo pealeii*. Stimulus: touch (and visual stimulus of impending touch). Response: escape jetting and ink release.
- ⁶⁸*C. elegans*, *Caenorhabditis elegans*. Stimulus: odor. Response: avoidance.
- ⁶⁹Leech, *Hirudo medicinalis*. Stimulus: touch. Response: bending reflex.
- ⁷⁰Earthworm, *Lumbricus terrestris*. Stimulus: light and vibration. Response: shortening reflex.
- ⁷¹Polychaete, Stimulus: light and shock. Response: withdrawal response.

TABLE 1 | Footnote Continued

- ⁷²Sea slug, *Aplysia californica*. Stimulus: touch. Response: withdrawal.
- ⁷³Sea slug, *Aplysia californica*. Stimulus: touch. Response: withdrawal.
- ⁷⁴Sea slug, *Tritonia diomedea*. Stimulus: chemical—NaCl. Response: swimming response.
- ⁷⁵Pond snail, *Physa acuta*, *P. heterostropha*, and *P. gyrina*. Stimulus: light, mechanical shock and electrical shock. Response: withdrawal.
- ⁷⁶Flatworm, *Dugesia dorotocephala*. Stimulus: cocaine. Response: hyperactivity—number of c-like movements.
- ⁷⁷Starfish, *Luidia clathrata*. CS: darkness. US: food. Behavior: food search (normally done in light).
- ⁷⁸Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: proboscis extension response.
- ⁷⁹Honeybee, *Apis mellifera*. CS: heat—applied via water to antennae. US: sucrose. Behavior: proboscis extension response.
- ⁸⁰Honeybees, *Apis mellifera*. CS: vibration or airpuff. US: shock. Behavior: avoidance of shock by temporary interruption of feeding—releasing from feeder momentarily. This study was the first to show latent inhibition in honeybees—that preexposure to the CS retarded conditioning.
- ⁸¹Cockroach, *Periplaneta americana*. CS: odor. US: sucrose or NaCl. Behavior: visiting odor source.
- ⁸²Drosophila, *Drosophila melanogaster*. CS: odor. US: shock. Behavior: odor avoidance.
- ⁸³Ant, *Myrmica sabuleti*. CS: colored shapes or odor. US: sucrose. Behavior: approaching and drinking sucrose.
- ⁸⁴Ant, *Cataglyphis fortis*, *Melophorus bagoti*. CS: color—black and white visual stimuli in a decision chamber. US: access to entrance—transport by human back to nest. Behavior: approaching visual stimuli.
- ⁸⁵Bumblebee, *Bombus terrestris*. CS: odor. US: sucrose. Behavior: proboscis extension response.
- ⁸⁶Cricket, *Gryllus bimaculatus*. CS: odor. US: sucrose or NaCl. Behavior: visiting odor source.
- ⁸⁷Blowfly, *Phormia regina*. CS: water and saline. US: sucrose. Behavior: proboscis extension response.
- ⁸⁸Hawkmoth, *Manduca sexta*. CS: odor. US: sucrose. Behavior: cibarial pump reflex measured by electrophysiological recordings of their cibarial pump muscle.
- ⁸⁹Locust, *Schistocerca gregaria*. CS: odor. US: food. Behavior: opening of their maxillary palps.
- ⁹⁰Wasp, *Microplitis croceipes*. CS: host—host faeces. US: odor—natural, vanilla or unattractive. Behavior: host-seeking flight responses.
- ⁹¹Butterfly, *Battus philenor*. CS: two different colors. US: presence of host plant leaf extract and presence of sucrose. Behavior: oviposition and feeding.
- ⁹²Crab, *Chasmagnathus granulatus*. CS: light and dark compartments. US: food. Behavior: exploratory behavior.
- ⁹³Crab, *Chasmagnathus granulatus*. CS: context—specific changes in light patterns within testing area (box). US: opaque figure ahead. Behavior: escape response—quantified via microphones recording amount of vibrations within box.
- ⁹⁴Crayfish, *Procambarus clarkii*. CS: toxic chemical. US: food. Behavior: food avoidance.
- ⁹⁵Lobster, *Panulirus argus*. CS: food odor. US: predator odor. Behavior: food avoidance.
- ⁹⁶Spider, *Phidippus princeps*. CS: color cues. US: food—prey. Behavior: approaching food.
- ⁹⁷Spider, *Hasarius adansonii*. CS: colored paper. US: heat—part of floor via hotplate. Behavior: avoidance of color.
- ⁹⁸Whip spider, *Phrynos marginemaculatus*. CS: coarse and fine tactile cues. US: refuge—holes in floor. Behavior: escape to refuge in response to bright light.
- ⁹⁹Horseshoe crab, CS: light. US: shock. Behavior: tail-spine movement measured by a kymograph and a string attached to the tail-spine.
- ¹⁰⁰Octopus, *Octopus vulgaris*. CS: visual orientation of shapes. US: food. Behavior: attacking food.
- ¹⁰¹Cuttlefish, *Sepia officinalis*. CS: plastic spheres. US: food. Behavior: attacking food (autoshrinking with spheres).
- ¹⁰²*C. elegans*, *Caenorhabditis elegans*. CS: ion solutions—Na⁺ or Cl⁻. US: food—*E. coli*. Behavior: presence near stimulus.
- ¹⁰³*C. elegans*, *Caenorhabditis elegans*. CS: acetic acid. US: odor of diacetyl (organic volatile molecule they are attracted to). Behavior: tracking/avoiding diacetyl.
- ¹⁰⁴Leech, *Macrodelia ditetra*. CS: light. US: shock. Behavior: contraction or extension.

TABLE 1 | Footnote Continued

- ¹⁰⁵Leech, *Hirudo medicinalis*. CS: touch. US: shock. Behavior: shortening reflex. This study showed that latent inhibition occurs in the leech during classical conditioning. If leeches were preexposed to the CS, learning was degraded.
- ¹⁰⁶Earthworm, *Lumbricus terrestris*. CS: light. US: vibration from loudspeaker. Behavior: extend their anterior body segments.
- ¹⁰⁷Sea slug, *Aplysia californica*. CS: light touch to siphon. US: strong electric shock to tail. Behavior: contraction of whole body.
- ¹⁰⁸Sea slug, *Aplysia californica*. CS: light touch to lip. US: food. Behavior: biting.
- ¹⁰⁹Pond snail, *Lymnaea stagnalis*. CS: light touch to lip. US: electrophysiological stimulation of a modulatory interneuron. Behavior: fictive feeding movements.
- ¹¹⁰Land snail, *Limax maximus*. CS: food odor. US: quinine (bitter tasting solution) on food. Behavior: avoidance of food.
- ¹¹¹Flatworm, *Dugesia dorotocephala*. CS: light. US: shock. Behavior: sharp turning and contraction of body.
- ¹¹²Sea anemone, *Cribrina xanthogrammica*. CS: light. US: shock. Behavior: folding of oral disc and tentacles.
- ¹¹³Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: Proboscis extension.
- ¹¹⁴Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: Proboscis extension.
- ¹¹⁵Cockroach, *Periplaneta americana*. CS: home cage (safety). US: shock. Behavior: running to home-cage.
- ¹¹⁶Drosophila, *Drosophila melanogaster*. Flies learned to solve a T-maze using odors to avoid shock.
- ¹¹⁷Ant, *Formica subsericea* and *Formica exsectoides*. Ants learned to solve a maze between foraging and returning home.
- ¹¹⁸Moth, *Macroglossum stellatarum*. CS: color. US: sucrose. Behavior: feeding.
- ¹¹⁹Locust, *Schistocerca gregaria*. Locusts learned to solve a T-maze to find food using the color of the walls.
- ¹²⁰Butterfly, *Battus philenor*. CS: color. US: sucrose. Behavior: feeding.
- ¹²¹Crab, *Gecarcinus lateralis*. CS: safety. US: water. Behavior: escape response in a spatial situation.
- ¹²²Crayfish, *Orconectes propinquus*. Crayfish learned to solve a T-maze to get to a comfortable situation (wet/cool) and avoid a negative situation (hot/dry) using spatial configuration.
- ¹²³Lobster, *Homarus americanus*. Lobsters learned to grip a sensor bar when presented with light of different intensities to obtain food.
- ¹²⁴Octopus, *Octopus vulgaris*. CS: shapes. US: food. Behavior: food attack response.
- ¹²⁵Cuttlefish, *Sepia officinalis*. Cuttlefish learned to escape a maze.
- ¹²⁶Earthworm, *Lumbricus terrestris*. Earthworms learned to solve a T-maze using light, touch and shock as reinforcers.
- ¹²⁷Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: proboscis extension.
- ¹²⁸Honeybee, *Apis mellifera*. Honeybees learned to discriminate flowers using odors.
- ¹²⁹Honeybee, *Apis mellifera*. Honeybees learned to discriminate flowers using complex mixtures of odors.
- ¹³⁰*C. elegans*, *Caenorhabditis elegans*. Stimulus: chemical. Response: withdrawal.
- ¹³¹Honeybee, *Apis mellifera*. Honeybees learned to discriminate artificial flowers based on color to obtain sucrose.
- ¹³²Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: proboscis extension.
- ¹³³Honeybee, *Apis mellifera*. CS: odor. US: sucrose. Behavior: proboscis extension.
- ¹³⁴Bumblebee, *Bombus impatiens*. Bumblebees learned to discriminate artificial flowers based on color hue to obtain sucrose.
- ¹³⁵Moth, *Manduca sexta*. CS: odor. US: sucrose. Behavior: feeding response.
- ¹³⁶Honeybees, *Apis mellifera*. Honeybees learned to touch silver plates with their antennae (more frequently) to obtain sucrose.
- ¹³⁷Cockroach, *Periplaneta americana*. Cockroaches learned to move their leg to a specific position in order to avoid a shock.
- ¹³⁸Drosophila, *Drosophila melanogaster*. Drosophila learned to turn their body (via wing movement) to avoid heat applied to one side of their body.
- ¹³⁹Drosophila, *Drosophila melanogaster*. Drosophila learned to move their leg to a specific position in order to avoid a shock.
- ¹⁴⁰Drosophila, *Drosophila melanogaster*. Drosophila learned to move their leg to a specific position in order to avoid heat.

TABLE 1 | Footnote Continued

¹⁴¹Ant, *Myrmica sabuleti*.Ants learned to find food in an apparatus.

¹⁴²Ant, *Myrmica sabuleti*.Ants learned to use odors to navigate and find food.

¹⁴³Bumblebees, *Bombus terrestris*.Bumblebees learned to land on artificial flowers that possessed conspecifics in order to obtain reward from the flower.

¹⁴⁴Cricket, *Zealandosandrus gracilis*.Crickets learned to move their body and leg into a specific position in order to turn off an aversive loud sound.

¹⁴⁵Blowfly, *Protophormia terrae novae*.Blowflies learned to enter and reenter a hole to obtain food.

¹⁴⁶Hawkmoth, *Manduca sexta*.Hawkmoths learned to probe at odorless feeders to obtain reward.

¹⁴⁷Locust, *Schistocerca americana*.Locusts learned to move their leg to a specific position in order to avoid heat applied to their head.

¹⁴⁸Crab, *Carcinus maenas*.Crabs learned to suppress natural eye extension after withdrawal reflex through aversive training with an air puff.

¹⁴⁹Crab, *Carcinus maenas*.Crabs learned to press a lever to obtain food.

¹⁵⁰Crayfish, *Procambarus elarkii* and *Cambarus diogenes*.Crayfish learned to move their claw to a specific position in order to avoid a shock.

¹⁵¹Crayfish, *Procambarus clarkii*.Crayfish learned to pull a lever for food.

¹⁵²Crayfish, *Procambarus clarkii*.Crayfish learned to walk forward to avoid a shock rather than naturally tail-flipping.

¹⁵³Lobsters, *Homarus americanus*.Lobsters learned to apply force with their claw to a sensor bar to obtain food.

¹⁵⁴Octopus, *Octopus cyanea*.Octopi learned to move down a runway to obtain food.

¹⁵⁵Octopus, *Octopus cyanea*.Octopi learned to extend their arm into a tube and out of the water in order to obtain food.

¹⁵⁶Sea slug, *Aplysia californica*.Aplysia learned to bite to receive electrophysiological stimulation to the anterior branch of the esophageal nerve (which presumably conveys information about the presence of food during ingestive behavior).

¹⁵⁷Pond snail, *Lymnaea stagnalis*.Snails learned to suppress their aerial respiratory behavioral drive through aversive training with touch.

¹⁵⁸Pond snail, *Lymnaea stagnalis*.Snails learned to suppress their naturally occurring behavior of escape from a water tank through aversive training with KCl.

¹⁵⁹Honeybees, *Apis mellifera*.Honeybees learned that when a certain color was presented to them, one odor predicted sucrose reward and another predicted no reward. However, when a different color was presented, these relationships switched.

¹⁶⁰Honeybees, *Apis mellifera*.Honeybees learned that specific scents were rewarding at specific times of the day.

¹⁶¹Honeybees, *Apis mellifera*.Honeybees learned that artificial flowers of a certain color were rewarding on certain times of the day and that they had to approach these flowers from a certain angle in order to obtain reward—land on a specific petal first.

¹⁶²Honeybees, *Apis mellifera*.Honeybees learned that in one of two identical (outside and inside) huts sucrose was located between two yellow cylinders, while in the other the sucrose was located between two blue cylinders.

¹⁶³Honeybee, *Apis mellifera*.Honeybees learned that different colored checkered patterns alone were predictive of reward, but when paired together they were not rewarding.

¹⁶⁴Honeybee, *Apis mellifera*.Honeybees learned that certain odors alone were predictive of a reward, but together they were not.

¹⁶⁵Cockroach, *Periplaneta americana*.Cockroaches learned to associate one odor (vanilla) with water and another (peppermint) with saline under illumination, but in the dark to associate the opposite—vanilla with saline and peppermint with water.

¹⁶⁶Drosophila, *Drosophila melanogaster*.Drosophila learn that in one context (presence of a specific color—green) one of two different patterns (“T” or inverted “T”) predict punishment, while in a different context (presence of a different color—blue) this predictive relationship is switched.

¹⁶⁷Ant, *Camponotus aethiops*.Ants learned to associate a certain cuticular hydrocarbon profile (the scent of an ant from another colony) with food reward and approached the food accordingly. But when another ant was present the profile indicated an ‘enemy’ ant and became aggressive.

¹⁶⁸Bumblebee, *Bombus terrestris*.Bumblebees learned to approach one of a pair of patterns (a 45° grating) and to avoid the other (a 135° grating) to reach a feeder, and to do the opposite to reach their nest (approach a 135° grating and avoid a 45° grating).

¹⁶⁹Cricket, *Gryllus bimaculatus*.Crickets learned to associate one odor (vanilla) with water and another (peppermint) with saline under illumination, but in the dark to associate the opposite—vanilla with saline and peppermint with water.

TABLE 1 | Footnote Continued

¹⁷⁰Lobster, *Panulirus argus*.Lobsters learned through aversive conditioning to not search for food when presented with a mixture of two food-related odors (AX). However, they could still learn that when either odor was separately presented with a novel odor (AY or XY), they could search for food without aversive reinforcement.

¹⁷¹Honeybee, *Apis mellifera*.Honeybees learned to discriminate visual patterns that contained two and three elements and without any further training generalized this discrimination to patterns with three and four elements.

¹⁷²Honeybee, *Apis mellifera*.Honeybees learned that a feeder was located between the third and fourth landmark in a series of landmarks that changes size and position.

¹⁷³Honeybee, *Apis mellifera*.Honeybees learned to stop and receive a reward after passing a specific number of landmarks and to generalize this to novel landmarks.

¹⁷⁴Beetle, *Tenebrio molitor*.Mealworms learned to discriminate filter papers containing odors from one or three females and from one or four females.

¹⁷⁵Review of arthropod navigation.

¹⁷⁶Navigation in lobsters.

¹⁷⁷Review of cephalopod navigation.

¹⁷⁸Honeybee, *Apis mellifera*.Honeybees learned to solve a delayed matching to sample task, where they had to respond to a stimulus that matched a previously encountered stimulus. They also learned to grasp the opposite relationship, difference, by responding to the sample that was different than a previous stimulus.

¹⁷⁹Honeybee, *Apis mellifera*.Honeybees learned the concept of above/below by discriminating between visual targets that were above or below a reference bar in order to receive reward.

¹⁸⁰Bumblebee, *Bombus terrestris*.Bumblebees learned in a task where they had to choose between two pairs of stimuli, that the two colors or patterns that were identical predicted reward.

Note: Invertebrate groups are ordered phylogenetically (phylogeny from Mallatt et al. 182). Learning types are grouped by supposed complexity of learning phenomena.

Invertebrates comprise over 95% of the earth’s animal population, in terms of numbers of individuals and species. They are tremendously diverse and extant species span an enormous range of body plans and types of nervous systems, from simple nerve nets to complex cephalized systems. For these reasons invertebrates have also been the focus of comparative research exploring the evolution of learning and cognition.

Our purpose here is not to give a full review of invertebrate learning, which would take far too much space. Rather, we will sketch what is known of the range of learning phenomena documented in the invertebrates. We highlight the gaps that need to be filled for a true comparative analysis of learning abilities across invertebrates, and suggest directions for future research on learning. Our main arguments are that the current approach to comparative learning research:

1. is not properly comparative enough and focuses too much on a skewed species range.
2. is reliant on a phenomena-based classification of learning that assumes levels of relative complexity of learning phenomena that may not reflect the underlying neural mechanisms. We discuss examples of how forms of cognitive learning can be supported by the same basic circuitry as habituation and associative learning,

and therefore from a mechanistic perspective it is not clear which form of learning is the more complex.

3. does not pay enough attention to the neurobiology of how animals actually do things. An important objective of modern neuroscience is to understand learning in terms of changes in nervous systems rather than simply behavioral phenomena. Outside of the classic model systems (*Drosophila*, *Aplysia*, *Apis mellifera* and *Caenorhabditis elegans*) mechanistic studies of invertebrate learning are rather lacking. We make the case that by incorporation of neurobiology into comparative studies of learning, we can better understand which abilities are independent of each other, which are truly more complex than others and thereby gain a better perspective on how forms of learning have evolved.

COMPARATIVE STUDIES OF INVERTEBRATE LEARNING

In Table 1, we have summarized the enormous variety of learning phenomena (see Box 1) documented in different invertebrate groups. Two historical research traditions have contributed to the modern study of invertebrate learning. The largely North American studies of animal learning stemming from the pioneering work of Thorndike¹⁸⁴ and Skinner¹⁸⁵ provided standard equipment, such as the operant chamber, and experimental procedures, such as the classical conditional paradigm^{185,186} by which several now-classic forms of learning phenomena were defined. Focusing on a few vertebrate systems (rats, pigeons, primates) in highly controlled, albeit artificial, laboratory conditions a catalog of types of learning has emerged. A good chunk of invertebrate learning research involves adapting this mode of research and the philosophy of distinct learning paradigms to various invertebrate animals. From crabs in operant chambers to bees in classical conditioning paradigms, efforts to replicate the traditional vertebrate research are immense.

BOX 1

DEFINITIONS OF TERMS

Habituation decrease in a physiological response to a stimulus as a result of repeated exposure to that stimulus.

Sensitization increase in a physiological response to a stimulus as a result of repeated exposure

to that stimulus or exposure to some unrelated stimulus (e.g., shock).

Classical/Pavlovian conditioning learning to respond to a neutral (conditioned) stimulus by associating it with another stimulus (unconditioned) that elicits a physiological response.

Concept learning learning about relations between objects (e.g., same/different, above/below) rather than about absolute physical features (e.g., color, shape).

Contextual learning learning that in context 1 stimulus A is rewarded while stimulus B is not (AC1+ and BC1–), whereas it is the opposite in context 2 (AC2– and BC2+). Here, we consider negative-pattern discrimination as a type of contextual learning if one assumes that another similar stimulus may set a context (Table 1).

Operant/instrumental conditioning learning that a specific positive or negative result or outcome is associated with a specific voluntary behavior.

Nonelemental learning forms of learning that go beyond simple nonassociative learning or associative learning with links between two stimuli (classical conditioning) or between a stimulus and a response (operant conditioning).

Reversal learning learning a discrimination task with particular reinforcement contingencies and subsequently learning the same task but with the reinforcement contingencies reversed.

Peak shift phenomenon where an animal is first trained to respond to a positively reinforced stimulus (S+) and withhold responding to an unreinforced or punished stimulus (S–) that is similar to but not identical to the positively reinforced stimulus. Then, when tested without reinforcement on a continuum of stimuli including S+ and S–, animals show a maximal response not to the S+ but to a stimulus similar to S+ and yet more distinct from S–.

Proboscis extension response (PER) conditioning is one of the most important classical conditioning paradigms for exploring invertebrate (insect) learning. The assay was developed in honeybees^{187–189} but has since found utility with blow flies (*Phormia regina*),¹⁹⁰ bumble bees,⁸⁵ and *Drosophila*.¹⁹¹ PER has most often been used to examine associative conditioning of odor stimuli with sugar or salt in a classical associative conditioning paradigm. Indeed, almost everything we know of the neurobiology of odor learning in honeybees has come from studies using this paradigm.^{189,192}

For olfactory PER conditioning, animals are restrained such that they can only move their

mouthparts and antennae (and sometimes the head). Conditioned stimuli can then be presented to the animal in a very controlled way paired with various unconditioned stimuli. Presentation of a droplet of sucrose to the antennae and/or mouthparts is used as a reward. In some studies odors have additionally been paired with an absence of sugar reward, or concentrated salt solution touched to the antennae, or electroshock as punishment. The response measured is the occurrence of proboscis extension (reward) or withholding (punishment) to the conditioned stimulus (CS).¹⁸⁹

Several operant conditioning paradigms have also been developed for invertebrates¹⁹³ of which some notable ones are operant training of *Drosophila* flight direction in a tethered ‘flight simulator’ in which flies learn to turn to avoid an infra-red heat stress.^{138,194} Feeding behavior in the marine mollusc *Aplysia* can also be operantly conditioned with an appetitive protocol.^{195,196}

From this tradition of laboratory analyses of simple associative learning has emerged the modern discipline of animal cognition or comparative cognition¹⁹⁷ in which learning forms considered to involve more than elementary associations have been studied in carefully controlled laboratory assays. Areas of investigation include studies of spatial cognition, numerical competence, timing, and others. An investigation of the possible cognitive abilities of invertebrates has become a significant research theme.

The second research tradition that has contributed to invertebrate learning research is the, originally largely European, classical ethology,^{198,199} where animals and their behavior are studied in their natural habitats. Their learning abilities are inferred by devising experiments under field conditions. Some studies of invertebrate learning, for example, most of invertebrate navigation, reflects this tradition. Although very limited, some efforts have also been made to blend both traditions.

We will first describe the main types of learning (Box 1), focusing on the phylogenetic distribution of research within invertebrates and the resultant gaps in a true phylogenetic analysis.

NONASSOCIATIVE LEARNING

Nonassociative learning is considered the simplest form of learning. It consists of changes in responding to the same (kind of) stimulus either as a result of repeated presentations of that stimulus or else as a function of some other kind of event that is not associated with the stimulus. Classic forms of nonassociative learning are habituation, the waning

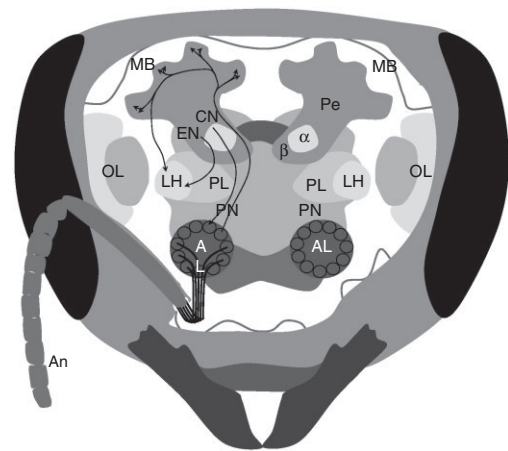


FIGURE 1 | Honeybee brain schematic highlighting the olfactory system. When odors are sensed by the antennae (An) odorant information is transferred via the antennal nerve to the antennal lobe (AL). Within the AL olfactory neurons synapse with projection neurons (PN) and interneurons within spherical glomeruli. PNs convey odor information as a cross-fiber code to the lateral horn and the calyces of the mushroom bodies (MB) where PNs synapse with the intrinsic neurons of the MBs, the Kenyon cells. Kenyon cells output via the α -lobe (α) and β -lobe (β). In these regions, Kenyon cells synapse with extrinsic neurons (EN) which connect the MBs with the lateral horn (LH) of the protocerebral lobe (PL) and other regions. Centrifugal neurons (CN) also send feedback information to the antennal lobes.

of responding, and sensitization, an increase in responding. Since these are learned changes in regard to a single stimulus only, they are considered the simplest possible learning phenomena.

All invertebrates so far reported, have shown both habituation and sensitization in some modality (Figure 1). From a defensive response to tactile stimulation in earthworms, to an odor-induced leg withdrawal in fruit flies, to an escape response from light in squids, habituation and sensitization seem integral behavioral mechanisms of all motile animals. It is noteworthy that animals with some of the simplest nervous systems known are able to demonstrate forms of nonassociative learning. Rotifers, microscopic invertebrates that contain only about 200 neurons²⁰⁰ (considerably less than even the much studied nematode *C. elegans*) were shown to reduce their contractile response to repeated tactile stimulation over time.^{52,54}

Sea squirt (tunicate) larvae,¹ which possess only about 100 neurons,²⁰¹ also display forms of nonassociative learning. Although as adults, these tunicates are sessile, the larval stages are commonly motile. Sea squirts are one of the closest invertebrate relatives to vertebrates; belonging to the Chordates, tunicates form a sister group to vertebrates. Upon light cessation, sea squirt larvae begin to swim and with light exposure they stop swimming. With

repeated exposure to light, these behaviors showed both habituation (weaker responses over time), and sensitization (increased responses over time), depending on the intensity of light.¹

How does the nervous system produce nonassociative forms of learning? It seems that a neural system can produce habituation and sensitization in a variety of ways. In the well-studied defensive reflexes in the sea slug *Aplysia*, nonassociative learning is accompanied by an alteration in post-synaptic potentials in sensory-motor synapses. This change in synaptic efficacy results from a decrease in transmitter release by presynaptic cells.²⁰² Sensitization, in contrast, involves an increase in neurotransmitter release.²⁰³ Research in *Aplysia* has shown how forms of nonassociative learning can be caused by changes at a single synapse, but this does not necessarily mean that all observed learning forms classified as nonassociative learning need necessarily be caused by this single mechanism.

BASIC ASSOCIATIVE LEARNING

In associative learning, an animal learns that a response or stimulus is associated with a given event or consequence. Two types of associative learning are classical (Pavlovian) conditioning¹⁸⁶ and operant (instrumental) conditioning.^{184,185} Classical conditioning involves learning the relationships between stimuli, whereas operant conditioning involves learning about the consequences of one's own behavior. Both have been reported for a wide range of invertebrate animals (Table 1). In classical conditioning, animals learn a predictive link between two events, typically a neutral stimulus, also known as the CS, and a biologically significant unconditioned stimulus (UCS). An example would be when sugar (UCS) is associated with the presentation of light (neutral CS) such that post-training animals show an appetitive response to the light stimulus alone. As a phenomenon, classical conditioning is generally thought of as more complex than nonassociative forms of learning because classical conditioning involves learning a relation between two things, rather than learning about a single stimulus. But classical conditioning is considered simpler than operant conditioning phenomena as in operant (instrumental) conditioning, animals learn that a voluntary physical response is associated with a specific UCS. An example might be when a rat learns to press a lever for a food reward. Classical and operant conditionings are considered distinct forms of learning, with operant conditioning as the more complex because it includes a classical component.^{204,205}

Many invertebrate animals exhibit classical conditioning, from ants, spiders, and butterflies

learning associations between colors and presence of food to horseshoe crabs and leeches learning that light indicates shock (Table 1). A variety of arthropods have been explored for this type of learning, as well as annelids, nematodes, and molluscs. Far scarcer, but notable are the studies of platyhelminthes, echinoderms, and cnidarians as these groups contain species with extremely simple nervous systems.

Platyhelminthes, or flatworms, are relatively simple bilaterian, soft-bodied invertebrates with no body cavity. They are protostomes and related to annelids (round worms) and molluscs. Like these other invertebrates, the flatworm's nervous system is cephalized and they are very motile. Flatworms have shown classical conditioning by learning to contract their body to presentation of light after associating light with shock.¹¹¹ Unlike flatworms, echinoderms are from the deuterostome lineage and as such are more closely related to vertebrates. Echinoderms, such as starfish, sea cucumbers, and sea urchins have a radial nervous system lacking any central brain. Starfish normally explore and feed when it is light, but have been shown to associate darkness with the presence of food and can learn, through classical conditioning, to search for food when light is removed.⁷⁷

Cnidarians are one of the most basal animal groups. They are diploblastic, which means they have only two germ layers in blastula development rather than three like most other animals (including all other invertebrates and vertebrates) and lack endoderm and true muscles. Cnidarians have no brain or central nervous system, and their nervous system is a simple nerve net with interconnected sensory neurons that respond to various stimuli, such as odors or touch. With just this simple system, not only do jellyfish and sea anemone habituate to light touch to their body by contracting less and less over repeated exposure, but sea anemones show classical conditioning as well: they learn to contract their tentacles to presentation of light that predicts shock.¹¹² This would suggest that even a simple nerve net is sufficient to support some forms of classical conditioning.

A special case of classical conditioning that has been documented in several invertebrate groups is reversal learning, which is the reversal of contingencies after the first bout of training. For example, if an animal learned that blue indicated food and white indicated shock, a reversal learning stage would have the animal learn the opposite: white → food and blue → shock. Reversal learning has long been used as a measure of cognitive flexibility, given the requirement to learn new associations and suppress old associations. Many invertebrate species have shown reversal learning, including arthropods

(honeybees, bumblebees, cockroaches, fruit flies, ants, crickets, moths, locusts, butterflies, crabs, crayfishes, lobsters), annelids (earthworm), and gastropod molluscs (octopuses and cuttlefish) (Table 1).

Latent inhibition is another special case of classical conditioning that has been recently explored in invertebrates. Here, a stimulus that has been often presented alone requires more training to become a CS than does a novel stimulus. This phenomenon is widespread in vertebrates and has been suggested to have adaptive advantages, such that an animal is able to ignore stimuli that have previously had no predictive value. There have been few reports of latent inhibition in invertebrate species: while some early studies suggested that both honeybees and molluscs did not show latent inhibition, later works have provided evidence for it in honeybees and leeches and similar phenomena have been found in *C. elegans* and *Drosophila* (Table 1).

In operant conditioning, animals learn that their own action is associated with obtaining some outcome. That outcome could be escaping or avoiding something aversive such as a heat shock or a predator, or obtaining something of value to the animal such as food or sex. Operant conditioning is thought to be more complex because the behavioral response is considered voluntary rather than reflexive. Most invertebrate examples of operant conditioning are found in the arthropods or molluscs (Table 1). Octopuses, for example, can learn to move down a runway¹⁵⁴ or reach their arm through a tube out of the water¹⁵⁵ to obtain food. Pond snails have been conditioned to suppress their naturally occurring respiratory behavior through negative reinforcement,¹⁵⁷ *Drosophila* can be conditioned to modify their tethered flight behavior in a flight simulator^{138,194} to avoid heat shock, and crabs can be conditioned to modify their escape and search behavior.²⁰⁶ Evidence of operant conditioning is lacking, however, in the closely related nematodes, and in annelid species, such as leeches and earthworms (Table 1). Operant and classical conditionings have long been considered distinct learning forms,^{204,205} and invertebrate studies have now provided mechanistic support for this view in that in both *Drosophila* and *Aplysia* operant and classical conditionings involve different (but interacting) subcellular signaling pathways.^{194,196,207}

There have been many more reports of classical than operant conditioning in invertebrates. Given that these are operationally distinct processes it does not follow that animals shown to be capable of classical conditioning will necessarily be capable of operant conditioning. This issue is worthy of investigation, but a great hindrance to understanding the evolution

of learning is that it is not clear whether attempts at operant conditioning in these cases have never been made, or what negative results have gone unreported.

The associative learning framework is extremely powerful and generalizable. Pioneering work by Spence²⁰⁸ explained how learning about a specific stimulus will generalize to similar stimuli. Spence²⁰⁸ introduced the concept of generalization gradients, which have proved useful in explaining several phenomena related to associative learning such as peak shift. In peak shift, animals are trained to respond to a positively reinforced stimulus (S+), e.g., a color hue or odor mixture. Treatment animals are trained with the same S+ but are in addition required to withhold responding to an unreinforced or punished stimulus (S-) that is similar to but not identical to the positively reinforced stimulus. Both groups are then tested without reinforcement on a continuum of stimuli including S+ and S-. Having been trained with both S+ and S-, animals show a maximal response not to the S+ but to a stimulus similar to S+ and yet more distinct from S-. Honeybees, bumblebees, and moths have shown peak shift behavior (Table 1).¹³⁴ Peak shift is considered to occur as a consequence of animals learning different outcomes for two similar stimuli. It involves learning two separate things, but is thought to involve basic associative processes.

COMPLEX FORMS OF LEARNING

What counts as cognition or complex learning has not been well defined. In general, complex learning somehow goes beyond nonassociative learning and associative processes linking two stimuli (classical conditioning), or between a response and a stimulus/outcome (operant conditioning). These forms of learning are thought to be complex according to our intuitions about the tasks. We will argue that this can be misleading because the neural mechanisms that underlie 'simple' forms of learning might turn out to be capable of mediating other more complex forms. Further, several forms of 'complex' learning such as social learning²⁰⁹ and basic metacognition²¹⁰ have been argued to be comprehensible within the simpler framework of associative processes.

Navigation represents a complex form of learning involving a combination of both classical conditioning of landmark cues and operant conditioning of proprioceptive cues such as step counting for path integration. Among invertebrate animals, the eusocial hymenoptera, ants and bees, have been most utilized when studying the complex learning required in navigation. Most studies have taken place in the animals' natural habitats,²¹¹ following

the ethological tradition. Invertebrates use many different mechanisms to navigate, and reviews of insect navigation are plentiful,^{212–214} so that we will only discuss briefly their capabilities.

Insects use both landmark- and vector-based forms of navigation. Landmark-based navigation means using some terrestrial (usually visual) cues for heading to a goal, while vector-based navigation means keeping track of the straight-line distance and compass direction to its starting point, typically its nest, during outbound travel. This is also called path integration.²¹⁵ In path integration, experience during the outbound portion of a particular journey must form the basis for the homeward journey, which makes it akin to one-trial learning.²¹²

Navigating insects also learn a great deal about their terrestrial surrounding, at present a topic of much research. They use information such as the skyline panorama²¹⁶ to walk stereotypical routes.^{217,218} It is thought that initial forays known as learning walks²¹⁹ or learning flights^{220,221} help the insects learn the terrestrial visual surround although what is learned from learning walks or flights is unclear. Honeybees may also learn to use terrestrial visual cues to form what can be called a topographic map,²²² although such an interpretation is disputed.²²³

Almost all the work on invertebrate navigation has been done with arthropods and most with hymenoptera. Some recent work has investigated short-distance navigation in crustacea¹⁷⁷ and lobsters.¹⁷⁶ However, these surely cannot be the only invertebrates with stationary homes that must be returned to after foraging. Indeed, many invertebrates must travel from one place to another and somehow remember the way back, either to find food or to find home. In order to gain a better understanding of the evolution of navigational skills, effort must be made to study the navigational abilities in more diverse invertebrate phyla.

Besides feats of navigation, some invertebrates have shown other forms of complex learning. One well-studied example is contextual learning in which an animal must learn that the value of a stimulus depends on other (contextual) conditions, for example: A+/B– in one context (C₁), but A–/B+ in another context (C₂). Such learning is considered nonelemental because one cannot assign one fixed value to a stimulus. In the example, the animal needs to learn that the configurations of AC₁ and BC₂ are rewarding, whereas BC₁ and AC₂ are nonrewarding. This introduces ambiguity in terms of reinforcement outcome as each stimulus is both rewarded and nonrewarded. This is also considered intrinsically more complex than simple association

because the number of elements that must be learned is greater. Insects provide some very good examples of this type of learning (Table 1). Crickets and cockroaches can learn that different and conflicting odor–food associations apply under different light conditions.^{165,169} Ants, bumblebees, and honeybees have all displayed contextual learning using specific places, direction of flight, time of day, distinct odors, or sides of the body as contexts.^{224–227}

Honeybees can also learn abstract concepts.¹⁷⁸ In a match-to-sample task, a bee encounters a sample stimulus (e.g., blue or yellow color) in an entrance chamber of a Y-maze. When it later faces two comparison stimuli (e.g., blue and yellow), its task is to choose the color that matches the sample that they had just encountered. After learning the task with one pair of samples, honeybees can transfer the learned rule to other sample and comparison stimuli, including those in a different sensory modality. This transfer shows that they had learned the abstract rule of choosing the same stimulus: a concept of sameness. This form of learning is also considered inherently more complex than simple associative processes as a generalizable abstract property independent of the specific stimuli must be learned and acted on.

Other forms of complex learning have been shown in a few invertebrates, such as number-based learning, and several forms of concept learning (Table 1). But as the classification of learning types becomes more complex, efforts become focused on fewer and fewer species, and almost always on a few or single species of hymenopteran arthropods. Honeybees and ants have proven to be excellent models for studying complex learning. But we again call for far wider comparative research so that we may better establish which taxonomic units come up negative for different forms of learning and cognition. The reporting of negative results, such as the honeybee's failure to show transitive inference,²²⁸ as well as positive ones is essential for understanding the phylogenetic distribution of cognitive abilities and the evolution of complex learning.

Defining different forms of learning phenomena makes a useful starting point for the study of learning. However, classifying two learning phenomena as distinct does not imply that these phenomena are mechanistically independent. A simple neural mechanism may support multiple different forms of learning. Consequently, these different learning and cognitive capacities are unlikely to have evolved independently. To illustrate these points we focus on the well-studied circuitry of odor learning in honeybees, and show how this elementary neural mechanism can support multiple forms of learning and cognition.

THE HONEYBEE OLFACTORY LEARNING PATHWAY

The anatomy of the honeybee olfactory learning pathway has been well mapped²²⁹ (Figure 1). Approximately 50,000 olfactory sensory cells project from the periphery to the antennal lobes.²³⁰ The antennal lobes contain about 160 densely packed spherical neuropilar regions, the glomeruli. Antennal nerve cells form connections with dendrites of local interneurons, which synapse both within and between glomeruli, as well as about 950 projection neurons, which output to the mushroom bodies and lateral protocerebrum.²³¹ Axons from olfactory receptors sensitive to the same chemicals converge on the same glomerulus. Different odors activate different sets of glomeruli to varying degrees, and odor identity is encoded as a specific spatiotemporal pattern of output across the 950 projection neurons.^{232–234} Odor codes overlap in the projection neurons as the representation of each odor engages a relatively high proportion of the limited number of projection neurons.

The projection neurons form synaptic connections with dendrites of the 170,000 Kenyon cells within each of the two mushroom bodies. Responses of Kenyon cells to odors are highly selective,^{235–238} with a far smaller proportion of the Kenyon cell population responding to a given odor than the projection neuron population. In honeybees, axons of the Kenyon cells project to the α - and β -lobes of the mushroom bodies where they synapse with dendrites of small populations of extrinsic neurons. In the α -lobes of the mushroom bodies, Kenyon cells connect with just 400 extrinsic neurons, which output to various parts of the brain, including the premotor descending neuropil of the lateral horn.²³⁹ The extrinsic neurons are thought to organize motor responses based on the recognized odor, such as proboscis extension or retraction.^{240,241}

PLASTICITY IN THE HONEYBEE OLFACTORY LEARNING PATHWAY RELATED TO MULTIPLE DIFFERENT FORMS OF LEARNING

Although the honeybee olfactory learning pathway is structurally simple, it is highly plastic. Learning changes patterns of neural activity in response to odor stimuli at each level and these changes presumably reflect plastic changes in synaptic connectivity and/or excitability. Changes in antennal lobe and Kenyon cell neural activity have been seen as a result of nonassociative odor presentation, but the most pronounced changes have been seen following

association of an odor with reward or aversive stimulus, i.e., classical conditioning. Throughout this circuit, reward, punishment, or a lack of reward are encoded by neuromodulatory signals such as octopamine, dopamine, and γ -aminobutyric acid (GABA) released from specific cell populations.^{242–244} The actions of these neuromodulators contribute to long-term changes in synaptic strength between neurons in the circuit, and thereby learned changes in neural connectivity.^{192,243,245,246}

Processing of odors within the antennal lobe (AL) is highly plastic and modifiable by learning such that pairing odor stimuli with reward or punishment changes the odor coding within glomeruli and the projection neurons.^{233,247} Differential conditioning with two odors (one associated with reward and one unrewarded) causes the patterns of honeybee AL glomerular activation for the two odors to diverge, making the patterns for these odors more distinct after training.^{233,248,249} Additionally, overall activity for the reward-associated odor increases in both the antennal lobes²⁴⁸ and the projection neurons,²⁵⁰ resulting presumably in increased discriminability and possibly salience of rewarded odors.²⁴⁹

Plastic changes in odor coding are also found within the population of Kenyon cells in the mushroom bodies.²⁵¹ Nonreinforced odor presentations lead to a decrease in the strength of Kenyon cell responses to the odor, suggesting a neural correlate of a habituation-like process.²⁵¹ Presenting an odor paired with sucrose reward strengthens Kenyon cell responses.²⁵¹ Furthermore, associative conditioning of odor with sugar or water causes a change in the neural coding of odor within the Kenyon cell population with changes in coding being more pronounced for nonrewarded odors than for rewarded odors.²⁵¹ Both associative and nonassociative learning processes occur within the same population of neurons, and as in the antennal lobes the learned changes in neural activity serve to enhance neural responses to environmentally significant odor stimuli.

Mushroom bodies output to the extrinsic neurons where yet another layer of plasticity has been uncovered. With far fewer extrinsic neurons than Kenyon cells, each extrinsic neuron receives input from about 2000 Kenyon cells.²³⁹ Extrinsic neurons output to premotor areas and are important in organizing the behavioral response. Most extrinsic neurons have low stimulus specificity, typically showing some firing activity in response to a wide range of stimuli,^{239,240} but change their response profile as a consequence of olfactory learning.^{240,252–254} Following associative conditioning of an odor with sucrose as reward or water as punishment or

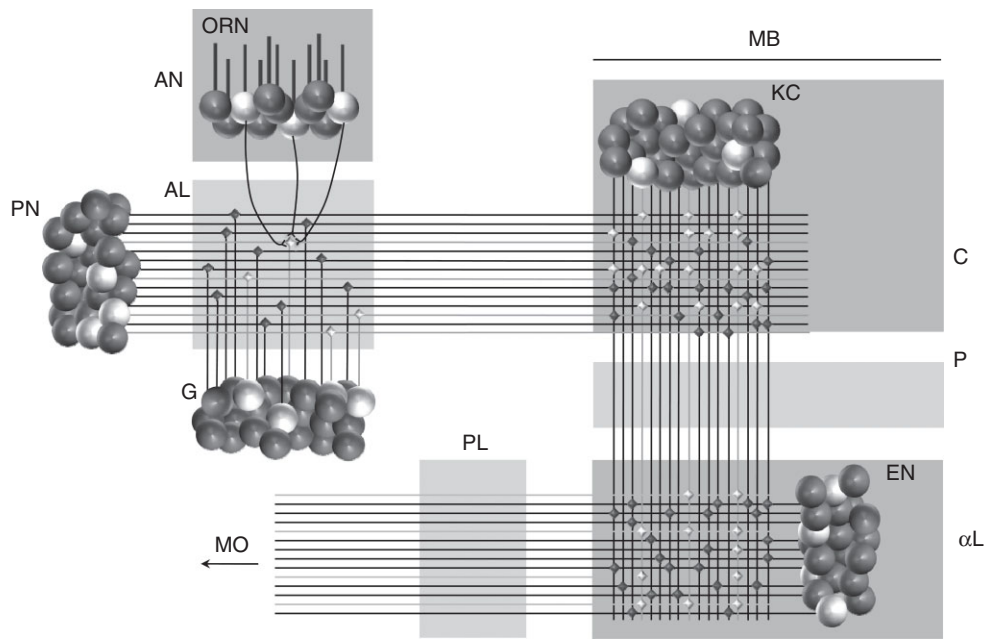


FIGURE 2 | Schematic of the honeybee olfactory learning pathway. Neuron cell bodies are shown as spheres, diamonds mark points of synaptic contact between projections. Lights gray neurons are active, dark gray inactive. The diagram highlights the organizational structure of the honeybee olfactory pathway as three serial connection matrices (1) between the olfactory receptor neurons (ORN) and the projection neurons (PN) within the glomeruli (G), (2) between the PN and the Kenyon cells (KC) within the calyx of the mushroom bodies (MB) and between the KC and extrinsic neurons (EN) within the lobes of the MB. The ENs output to premotor regions, including the lateral horn of the protocerebral lobe (PL), considered important for organizing the conditioned response. Odor information is encoded as a cross-fiber code within the PNs and KCs. Reward and punishment cause release of neuromodulators that change the pattern of activity within the KCs and ENs as a neural engram of the learning process.

deterrent, the population of neurons responding to a rewarded odor increases in number and intensity.²⁴⁰ The population of extrinsic neurons responding to odor paired with water also changes.²⁴⁰ These changes may be driven in part by learning related changes in odor coding in the upstream Kenyon cell population (described earlier), but also very likely reflect plasticity in the properties of the extrinsic neurons themselves.²⁴⁰ Because the extrinsic neurons terminate in premotor regions this neuron population is considered particularly important in determining and organizing the conditioned response to a stimulus, and plastic changes in the extrinsic neurons may contribute to learned changes in behavioral response.^{240,241,255}

HOW THE NEURAL ARCHITECTURE OF THE HONEYBEE OLFACTORY LEARNING CIRCUIT SUPPORTS MULTIPLE DIFFERENT FORMS OF LEARNING AND COGNITION

Learning involves first recognizing a specific stimulus and responding in a manner most appropriate to

the environmental consequence of the stimulus, which may be as simple as learning to not respond to inconsequential stimuli. The architecture of the bee brain appears to be exquisitely evolved to solve this general problem. The processing of olfactory stimuli in bees is structured as a series of three serially arranged neural codes within the projection neuron, Kenyon cell, and extrinsic neuron populations (Figure 2). Each population of neurons is serially connected by connection matrices. Connectivity in this pathway is initially divergent as odor information is passed from the compact code of the projection neurons to the sparse code of the Kenyon cells. It then converges as odor information progresses from the Kenyon cells to the extrinsic neurons. Huerta et al.²⁴¹ have argued that computationally, these are the optimal design principles for a self-organizing classifier of complex sensory information. The output of the classifier must be a consensus decision, and models of information processing suggest that a key mechanism by which such a consensus decision can emerge from a neuronal population is mutual inhibition.^{255–257} The most common form of mutual inhibition in neuron populations is lateral inhibition, where broadly ramifying inhibitory afferent connections link spatially proximate cells in a neuron

population. Lateral inhibition provides a mechanism to resolve competition among the extrinsic neurons to arrive at a single output.^{241,255} For example, if activity in extrinsic neurons causing proboscis extension exceeded that of extrinsic neurons causing proboscis retraction then the outcome of mutual inhibitory interactions between these neurons would be a single behavioral response: proboscis extension.

Organized in this way, the honeybee olfactory learning pathway could support multiple different forms of learning such as several different forms of olfactory PER conditioning (Figure 3). For simplicity, we consider the case of PER learning of odor and assume only two possible behavioral responses: activation of muscles that extend the proboscis or activation of muscles that withhold the proboscis. When not extended the bee proboscis needs to be actively supported in the retracted position, or actively retracted and then withheld.^{255,259–261}

It is assumed that the usual ‘default’ response to novel odors is withholding the proboscis. As a result of the synaptic plasticity described above, associative conditioning of an odor with sucrose reward will increase responses to the odor in extrinsic neurons causing proboscis extension. With enough activation of these extrinsic neurons, lateral inhibition then works to ‘silence’ the extrinsic neurons causing proboscis withholding, and conditioned proboscis extension can result. Conditioning with an aversive stimulus or an absence of reward will decrease activity in extrinsic neurons causing proboscis extension in response to the odor and increase activity in extrinsic neurons causing proboscis withholding.²⁵⁵ The degree of reorganization of synaptic weights in the extrinsic neuron population determines acquisition rate. Similar odors (or odor blends with components in common) activate more similar patterns of activity in projection neurons, Kenyon cells, and extrinsic neurons than do dissimilar odors (or blends).²⁵⁵

These simple assumptions, which are well supported by experimental data, have been the basis of a computational model of olfactory learning in the mushroom body circuit capable of habituation, association, and latent inhibition²⁵⁵ and we propose that conceptually the same circuit operation could explain phenomena of reversal learning and peak shift (Figure 3). The model assumes simply that learning occurs as a result of changes in the connectivity matrix linking a sensory representation to neurons organizing motor output. Second, the motor output occurs as the net output of a neuronal population self-organized by mutual inhibition within the population. Such a neurocomputational model may provide a neurophysiological instantiation of

Spence’s²⁰⁸ abstract gradients of excitation and inhibition underlying peak shift. These different learning phenomena then manifest as intrinsic properties of this circuit. The resulting inference is that if operationally defined learning phenomena can share neural circuitry it is very unlikely that different forms of learning evolved independently, and some forms of cognition considered complex in terms of information processing may be emergent properties of quite simple plastic connection matrices relating sensory input to motor output.

CONCLUSIONS

The simplicity of many invertebrate nervous systems has enabled tremendous progress to be made in analyzing mechanisms of learning and memory with various now-classic invertebrate model systems. Many of the identified mechanisms have been found to be conserved with vertebrates,²⁶² which further enhances the utility of studying invertebrate learning and raises some interesting questions about the evolutionary history of learning. But the potential of invertebrates for a true comparative and phylogenetic analysis of learning abilities has not been fully realized. We have emphasized the need for much wider comparisons of learning, in order to trace evolutionary roots. The same can be said of the comparison of nervous systems. Our approach to the study of the evolution of learning takes Domjan’s¹⁸¹ definition of learning to heart: learning is understood as changes in underlying mechanisms, specifically changes in neural activity and synaptic connectivity. Learning, as a cognitive capacity, should therefore evolve as changes in the capacity and connectivity of neural substrates. We suggest that the simple circuits available in honeybees, and no doubt many other invertebrates, can support various forms of learning. If this is true, many cognitive abilities are unlikely to have evolved independently because they can emerge from architecturally simple circuits serving what has been called basic learning. These simple circuits need not be any more complex than those required for simple nonassociative learning.

We argue that the study of comparative cognition needs to move beyond simple cataloging of what different species are capable of to examine how nervous systems actually solve different problems. In order to understand how cognition evolved we need to test basal groups across phyla, including cnidarians, echinoderms, and invertebrate chordates that have already been shown to have the neural circuitry required for nonassociative learning. Along with touting the cognitive abilities of animals with

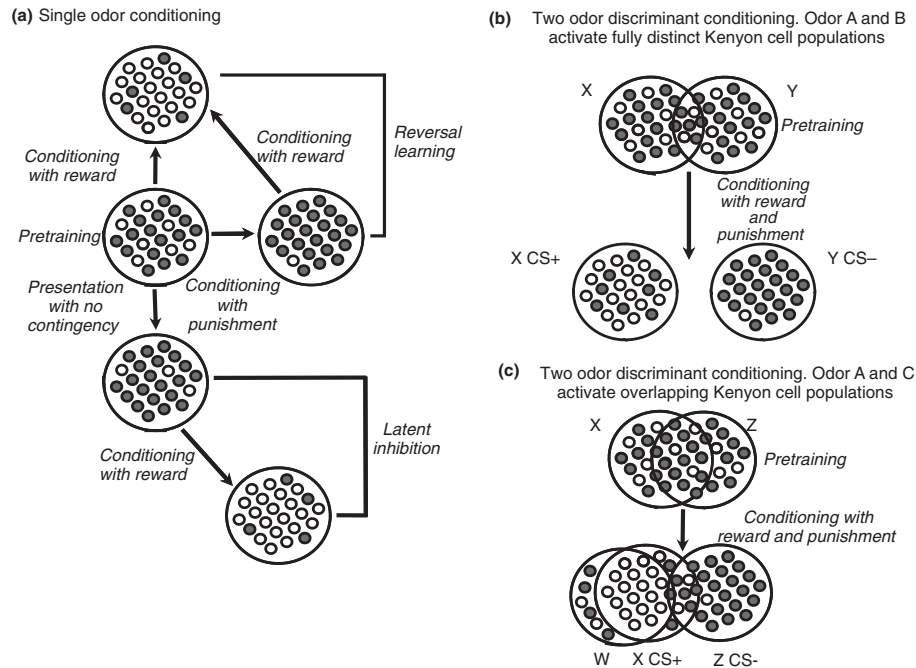


FIGURE 3 | This simple conceptual model of how different forms of learning can be supported by the same neural system is developed from a series of formal mathematical models of the bee olfactory learning pathway.^{255,257,258} Changes in the activity of extrinsic neurons (ENs) to odors drive both nonassociative and associative learning. The panels show the populations of ENs responding above threshold to a given odor, with neurons colored white activating proboscis extension, and neurons colored black activating proboscis retraction. Reciprocal lateral inhibition in this population makes the behavioral outcome of the inhibitory interactions into a 'winner takes all' situation, in which the behavioral response is determined by whether the extension or retraction groups are numerically dominant in the active EN population. The default response of ENs to an odor is that 'retraction' neurons dominate. Consequently bees do not normally extend their proboscis to a novel odor. (a). Single odor conditioning. After association of the odor with sucrose reward, the pattern of activation of ENs changes such that additional neurons of the proboscis extension group are recruited. The 'winner takes all' feature resulting from lateral inhibition results in, post-training, bees extending their proboscis to the odor. Associative conditioning with an aversive stimulus also changes the response of ENs to the odor such that fewer 'extension' neurons are activated and more 'retraction' neurons are activated. Repeated presentation of an odor alone with no consequence (habituation) causes similar, but less extreme, changes as training with an aversive stimulus.²⁵⁵ Latent inhibition describes the observation that appetitive conditioning with reward takes longer if animals have been first preexposed to the odor (CS) alone. This outcome is a natural consequence of the model because following preexposure of odor alone the number of extension group ENs activated by the odor is reduced, therefore requiring more conditioning trials with reward to bring the extension response to dominance²⁵⁵. For similar reasons, our model explains why the process of reversal learning (pairing an odor with reward after first pairing an odor with an aversive stimulus) is slower than simple appetitive conditioning: a greater shift in the pattern of active ENs is needed to bring proboscis extension to an odor to dominance in a reversal learning paradigm than in simple reward conditioning. (b) Discriminating two dissimilar odors. Odors X and Y are perceptually distinct and activate fully distinct populations of Kenyon cells. The compact nature of odor coding in the ENs results in some degree of overlap of EN populations responding to initial presentations of X and Y, meaning some neurons will respond to both odors. On initial odor presentation the retraction group dominates the response to both odors. Following differential conditioning of X with sucrose reward (CS+) and Y with an aversive stimulus (CS-) the populations of ENs responding to the two odors diverge. As a result of Hebbian processes extension group neurons are recruited to odor X, such that the extension group now dominates the EN response. The EN population responding to odor Y also shifts such that the retraction group is now even more dominant. (c) Discriminating two similar odors. Odors X and Z are perceptually similar and activate overlapping Kenyon cell populations. As a result, a significant number of extrinsic neurons will initially respond to both odors. Following differential conditioning to X (CS+) and Z (CS-), the extrinsic neuron populations activated by the two odors diverge, but cannot become completely distinct because of the high degree of odor similarity. For the extension EN neurons responding to both odors, strengthening of connections as a consequence of training with X is counteracted by training with Z. For the retraction EN neurons responding to both odors strengthening of connections as a consequence of training with Z is counteracted by training with X. These antagonistic processes will slow learning: it takes more training for the extension group to dominate the response to the CS+ odor X, and after training the extension group will dominate the response to X less than when following training with distinct CS+ and CS- in (b). This process also explains peak shift. After differential conditioning of similar stimuli, the maximal response occurs not to the CS+ odor X, but to a new odor (W) that is similar to X but more distinct from the CS- odor (Z). ENs responding to W are expected to overlap significantly with ENs responding to X, but overlap less with extrinsic neurons responding to Z. As a consequence of training with X and Z, the EN response to W may be more dominated by the extension group than the response to X. Consistent with empirical results, this interpretation suggests the occurrence of peak shift if X and Z (CS+ and CS-) are very similar. The distinct X and Y described in (b) would not produce peak shift.

simple neural architectures, we also need to report what these animals cannot do. The negative cases are required for inferring in which lineage or lineages a

trait might have arisen. This in turn is vital for our understanding of the limitations of any neural circuit and for piecing together how learning has evolved.

REFERENCES

1. Tsuda M, Kawakami I, Shiraishi S. Sensitization and habituation of the swimming behavior in ascidian larvae to light. *Zoolog Sci* 2003, 20:13–22.
2. Holmes S. Phototaxis in the sea urchin, *Arbacia punctulata*. *Anim Behav* 1912, 2:126–136.
3. von Uexkull J. Vergleichend sinnesphysiologische Untersuchungen. II. Der Schatten als Reiz für *Centrostephanus longispinus*. *Z Biol* 1896, 34:319–339.
4. Grave C. The tentacle reflex in a holothurian, *Cucumaria pulcherrima*. *Johns Hopkins Univ Circ* 1905, 178:24–27.
5. Braun G, Bicker G. Habituation of an appetitive reflex in the honeybee. *J Neurophysiol* 1992, 67:588–598.
6. Davis H, Heslop E. Habituation of hissing by Madagascar hissing cockroaches (*Gromphadorhina portentosa*): evidence of discrimination between humans? *Behav Process* 2004, 67:539–543.
7. Roeder KD. Organization of the ascending giant fiber system in the cockroach, *Periplaneta americana*. *J Exp Zool* 1948, 108:243–261.
8. Cho W, Heberlein U, Wolf FW. Habituation of an odorant-induced startle response in *Drosophila*. *Genes Brain Behav* 2004, 3:127–137.
9. Fischbach KF. Habituation and sensitization of the landing response of *Drosophila melanogaster*. *Naturwissenschaften* 1981, 68:332.
10. Duerr JS, Quinn WG. Three *Drosophila* mutations that block associative learning also affect habituation and sensitization. *Proc Natl Acad Sci U S A* 1982, 79:3646–3650.
11. Acevedo SF, Froudarakis EI, Kanellopoulos A, Skoulakis EMC. Protection from premature habituation requires functional mushroom bodies in *Drosophila*. *Learn Mem* 2007, 14:376–384.
12. Gailey DA, Jackson FR, Siegel RW. Male courtship in *Drosophila*: the conditioned response to immature males and its genetic control. *Genetics* 1982, 102:771–782.
13. Corfas G, Dudai Y. Habituation and dishabituation of a cleaning reflex in normal and mutant *Drosophila*. *J Neurosci* 1989, 9:56–62.
14. Langen TA, Triplet F, Nonacs P. The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. *Behav Ecol Sociobiol* 2000, 48:285–292.
15. Simonds V, Plowright CMS. How do bumblebees first find flowers? Unlearned approach responses and habituation. *Anim Behav* 2004, 67:379–386.
16. May ML, Hoy RR. Habituation of the ultrasound-induced acoustic startle response in flying crickets. *J Exp Biol* 1991, 159:489–499.
17. Bernard Thon AP. Differential sensitization, retention, and generalization of habituation in two response systems in the blowfly (*Calliphora vomitoria*). *J Comp Psychol* 1984, 98:119–130.
18. Wiel DE, Weeks JC. Habituation and dishabituation of the proleg withdrawal reflex in larvae of the sphinx hawk, *Manduca sexta*. *Behav Neurosci* 1996, 110:1133–1147.
19. Barrass R. A quantitative study of the behaviour of the male *Mormoniella vitripennis* (Walker) (Hymenoptera, Pteromalidae) towards two constant stimulus-situations. *Behaviour* 1961, 18:288–312.
20. Geva N, Guershon M, Orlova M, Ayali A. Memoirs of a locust: density-dependent behavioral change as a model for learning and memory. *Neurobiol Learn Mem* 2010, 93:175–182.
21. Szentesi A, Bernays EA. A study of behavioural habituation to a feeding deterrent in nymphs of *Schistocerca gregaria*. *Physiol Entomol* 1984, 9:329–340.
22. Rakitin A, Tomsic D, Maldonado H. Habituation and sensitization to an electrical shock in the crab *Chasmagnathus*. Effect of background illumination. *Physiol Behav* 1991, 50:477–487.
23. Hemmi JM, Merkle T. High stimulus specificity characterizes anti-predator habituation under natural conditions. *Proc Biol Sci* 2009, 276:4381–4388.
24. Walker I. Habituation to disturbance in the fiddler crab (*Uca annulipes*) in its natural environment. *Anim Behav* 1972, 20:139–146.
25. Krasne FB, Woodsmall KS. Waning of the crayfish escape response as a result of repeated stimulation. *Anim Behav* 1969, 17:416–424.
26. Chow K-L, Leiman AL. The photo-sensitive organs of crayfish and brightness learning. *Behav Biol* 1972, 7:25–35.
27. Daniel PC, Derby CD. Behavioral olfactory discrimination of mixtures in the spiny lobster (*Panulirus argus*) based on a habituation paradigm. *Chem Senses* 1988, 13:385–395.
28. George W, Peckham EG. Some observations on the mental powers of spiders. *J Morphol* 1887, 1:383–419.

29. Lahue R, Kokkinidis L, Corning W. Telson reflex habituation in *Limulus polyphemus*. *J Comp Physiol Psychol* 1975, 89:1061–1069.
30. Bullock A, McKeown C, Robertson M. Habituation and dishabituation to a vibrational stimulus by a millipede *Orthoporus texicolens*. *Trans Illinois State Acad Sci*, vol. 102; 2009.
31. Pieron H. *L'Evolution de la Memoire*. Flammarion; 1910.
32. Lagerspetz KYH, Kivivuori L. The rate and retention of the habituation of the shadow reflex in *Balanus improvisus* (Cirripedia). *Anim Behav* 1970, 18:616–620.
33. Kuba MJ, Byrne RA, Meisel DV, Mather JA. Exploration and habituation in intact free moving *Octopus vulgaris*. *Int J Comp Psychol* 2006, 19:1–426.
34. Long TM, Hanlon RT, Maat AT, Pinsker HM. Non-associative learning in the squid *Lolliguncula brevis* (Mollusca, Cephalopoda). *Mar Behav Physiol* 1989, 16:1–9.
35. Rankin CH, Beck CDO, Chiba CM. *Caenorhabditis elegans*: a new model system for the study of learning and memory. *Behav Brain Res* 1990, 37:89–92.
36. Ward S. Chemotaxis by the nematode *Caenorhabditis elegans*: identification of attractants and analysis of the response by use of mutants. *Proc Natl Acad Sci* 1973, 70:817–821.
37. Gee W. The behavior of leeches with special reference to its modifiability. *University of Calif Publ Zool* 1913, 11:197–305.
38. Stoller D, Sahley C. Habituation and sensitization of the shortening reflex in the leech, *Hirudo medicinalis*. *Society of Neuroscience Abstracts* 367, 1985.
39. Debski EA, Friesen WO. Habituation of swimming activity in the medicinal leech. *J Exp Biol* 1985, 116:169–188.
40. Kuenzer P. Verhaltenphysiologische Untersuchungen über das Zucken des Regenwurms. *Z Tierpsychol* 1958, 15:31–49.
41. Ratner SC, Gilpin AR. Habituation and retention of habituation of responses to air puff of normal and decerebrate earthworms. *J Comp Physiol Psychol* 1974, 86:911–918.
42. Johnson FN. The effects of temperature on the retention of photic habituation in the earthworm. *Life Sci* 1970, 9:1345–1351.
43. Nicol JAC. Responses of *Branchiomma vesiculosum* (Montagu) to photic stimulation. *J Mar Biol Assoc U K* 1950, 29:303–320.
44. Evans SM. Habituation of the withdrawal response in Nereid polychaetes. 1. The habituation process in *Nereis diversicolor*. *Biol Bull* 1969, 137:95–104.
45. Pinsker H, Kupfermann I, Castellucci V, Kandel E. Habituation and dishabituation of the gill-withdrawal reflex in *Aplysia*. *Science* 1970, 167:1740–1742.
46. Davis WJ, Mpitsos GJ. Behavioral choice and habituation in the marine mollusk *Pleurobranchaea californica* MacFarland (Gastropoda, Opisthobranchia). *Z Vergl Physiol* 1971, 75:207–232.
47. Frost WN, Brandon CL, Van Zyl C. Long-term habituation in the marine mollusc *Tritonia diomedea*. *Biol Bull* 2006, 210:230–237.
48. Cook A. Habituation in a freshwater snail (*Lymnaea stagnalis*). *Anim Behav* 1970, 178:463–474.
49. Crozier WJ, Arey LB. On the significance of the reaction to shading in chiton. *Am J Physiol* 1918, 46:487–492.
50. Pieron H. La loi de l'excitation lumineuse chez *Mya arenaria*. *C R Soc Biol* 1925, 93:1235–1238.
51. Humphrey G. Le Chatelier's rule, and the problem of habituation and dehabituation in *Helix albolabris*. *Psychol Forsch* 1930, 13:113–127.
52. Applewhite PB, Morowitz HJ. The micrometazoa as model systems for studying the physiology of memory. *Yale J Biol Med* 1966, 39:90–105.
53. Pearl R. *The Movements and Reactions of Fresh-water Planarians: A Study in Animal Behaviour*. London: J. & A. Churchill; 1903.
54. Applewhite PB. Non-local nature of habituation in a rotifer and protozoan. *Nature* 1968, 217:287–288.
55. Johnson MC, Wuensch KL. An investigation of habituation in the jellyfish *Aurelia aurita*. *Behav Neural Biol* 1994, 61:54–59.
56. Brace RC, Santer SJ. Experimental habituation of aggression in the sea anemone *Actinia equina*. *Hydrobiologia* 1991, 216–217:533–537.
57. Jennings HS. Modifiability in behavior. I. Behavior of sea anemones. *J Exp Zool* 1905, 2:447–472.
58. Kinoshita PT. Über den Einfluss mehrerer aufeinanderfolgender wirksamer Reize auf den Ablauf der Reaktionsbewegungen bei Wirbellosen. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere* 1911, 140:167–197.
59. DrnemWA N. Experimentelle sinnesphysiologische Untersuchungen an Coelenteraten. *Archiv für die gesamte Physiologie des Menschen und der Tiere* 1894, 57:495–550.
60. Hammer M, Braun G, Maelshagen J. Food-induced arousal and nonassociative learning in honeybees: dependence of sensitization on the application site and duration of food stimulation. *Behav Neural Biol* 1994, 62:210–223.
61. Zilber-Gachelin NF, Paupardin D. Sensitization and dishabituation in the cockroach. Main characteristics and localization of the changes in reactivity. *Comp Biochem Physiol A* 1974, 49:441–470.
62. McClung C, Hirsh J. Stereotypic behavioral responses to free-base cocaine and the development of behavioral sensitization in *Drosophila*. *Curr Biol* 1998, 8:109–112.

63. Walters ET, Illich PA, Weeks JC, Lewin MR. Defensive responses of larval *Manduca sexta* and their sensitization by noxious stimuli in the laboratory and field. *J Exp Biol* 2001, 204:457–469.
64. Kaiser L, Perez-Maluf R, Sandoz JC, Pham-Delegue MH. Dynamics of odour learning in *Leptopilina bouhardi*, a hymenopterous parasitoid. *Anim Behav* 2003, 66:1077–1084.
65. Aggio J, Rakitin A, Maldonado H. Serotonin-induced short- and long-term sensitization in the crab *Chasmagnathus*. *Pharmacol Biochem Behav* 1996, 53:441–448.
66. Krasne FB, Glanzman DL. Sensitization of the crayfish lateral giant escape reaction. *J Neurosci* 1986, 6:1013–1020.
67. Crook RJ, Lewis T, Hanlon RT, Walters ET. Peripheral injury induces long-term sensitization of defensive responses to visual and tactile stimuli in the squid *Loligo pealeii*, Lesueur 1821. *J Exp Biol* 2011, 214:3173–3185.
68. Kimura KD, Fujita K, Katsura I. Enhancement of odor avoidance regulated by dopamine signaling in *Caenorhabditis elegans*. *J Neurosci* 2010, 30:16365–16375.
69. Lockery SR, Kristan WB Jr. Two forms of sensitization of the local bending reflex of the medicinal leech. *J Comp Physiol A, Sens, Neural, Behav Physiol* 1991, 168:165–177.
70. Peeke HV, Herz MJ, Wyers EJ. Forward conditioning, backward conditioning, and pseudoconditioning sensitization in the earthworm (*Lumbricus terrestris*). *J Comp Physiol Psychol* 1967, 64:534–536.
71. Rullier F. La vision et l'habitude chez *Mercierella enigmatica* Fauvel. *Bull Lab Marit Dinard* 1948, 30:21–27.
72. Pinsker HM, Hening WA, Carew TJ, Kandel ER. Long-term sensitization of a defensive withdrawal reflex in *Aplysia*. *Science* 1973, 182:1039–1042.
73. Carew T, Castellucci V, Kandel E. An analysis of dishabituation and sensitization of the gill-withdrawal reflex in *Aplysia*. *Int J Neurosci* 1971, 2: 79–98.
74. Brown GD. Nonassociative learning processes affecting swimming probability in the seaslug *Tritonia diomedea*: habituation, sensitization and inhibition. *Behav Brain Res* 1998, 95:151–165.
75. Wells MJ, Wells J. Conditioning and sensitization in snails. *Anim Behav* 1971, 19:305–312.
76. Rawls SM, Patil T, Yuvashva E, Raffa RB. First evidence that drugs of abuse produce behavioral sensitization and cross-sensitization in planarians. *Behav Pharmacol* 2010, 21:301–313.
77. McClintock JB, Lawrence JM. Photoresponse and associative learning in *Luidia clathrata* Say (Echinodermata: Asteroidea). *Mar Behav Physiol* 1982, 9:13–21.
78. Takeda K. Classical conditioned response in the honey bee. *J Insect Physiol* 1961, 6:168–179.
79. Hammer TJ, Hata C, Nieh JC. Thermal learning in the honeybee, *Apis mellifera*. *J Exp Biol* 2009, 212:3928–3934.
80. Abramson CI, Bitterman ME. Latent inhibition in honeybees. *Anim Learn Behav* 1986, 14:184–189.
81. Watanabe H, Kobayashi Y, Sakura M, Matsumoto Y, Mizunami M. Classical olfactory conditioning in the cockroach *Periplaneta americana*. *Zool Sci* 2003, 20:1447–1454.
82. Quinn WG, Harris WA, Benzer S. Conditioned behavior in *Drosophila melanogaster*. *Proc Natl Acad Sci* 1974, 71:708–712.
83. Cammaerts M. Classical conditioning, temporal learning and spatial learning in the ant *Myrmica sabuleti*. *Biologia* 2004, 59:243–256.
84. Schwarz S, Cheng K. Visual associative learning in two desert ant species. *Behav Ecol Sociobiol* 2010, 64:2033–2041.
85. Laloi D, Sandoz J, Picard-Nizou A, Marchesi A, Pouvreau A, Tasei J, Poppy G, Pham-Delegue M. Olfactory conditioning of the proboscis extension in bumble bees. *Entomol Exp Appl* 1999, 90:123–129.
86. Matsumoto Y, Mizunami M. Olfactory learning in the cricket *Gryllus bimaculatus*. *J Exp Biol* 2000, 203:2581–2588.
87. Nelson MC. Classical conditioning in the blowfly (*Phormia regina*): associative and excitatory factors. *J Comp Physiol Psychol* 1971, 77:353–368.
88. Daly KC, Smith BH. Associative olfactory learning in the moth *Manduca sexta*. *J Exp Biol* 2000, 203:2025–2038.
89. PC S, Ott SR, Niven JE. Associative olfactory learning in the desert locust, *Schistocerca gregaria*. *J Exp Biol* 2011, 214:2495–2503.
90. Lewis WJ, Tumlinson JH. Host detection by chemically mediated associative learning in a parasitic wasp. *Nature* 1988, 331:257–259.
91. Weiss MR, Papaj DR. Colour learning in two behavioural contexts: how much can a butterfly keep in mind? *Anim Behav* 2003, 65:425–434.
92. Dimant B, Maldonado H. Habituation and associative learning during exploratory behavior of the crab *Chasmagnathus*. *J Comp Physiol A* 1992, 170:749–759.
93. Fustiñana MS, Carbó Tano M, Romano A, Pedreira ME. Contextual Pavlovian conditioning in the crab *Chasmagnathus*. *Anim Cogn* 2013, 16:255–272.
94. Arzuffi R, Salinas-Loera C, Racotta IS. Food aversion learning induced by lithium chloride in the crayfish *Procambarus clarkii*. *Physiol Behav* 2000, 68:651–654.
95. Fine-Levy JB, Girardot MN, Derby CD, Daniel PC. Differential associative conditioning and olfactory

- discrimination in the spiny lobster *Panulirus argus*. *Behav Neural Biol* 1988, 49:315–331.
96. Jakob EM, Skow CD. Jumping spiders associate food with color cues in a T-maze. *J Arachnol* 2007, 35:487–492.
 97. Nakamura T, Yamashita S. Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *J Comp Physiol A* 2000, 186:897–901.
 98. Santer RD, Hebets EA. Tactile learning by a whip spider, *Phrynus marginemaculatus* C.L. Koch (Arachnida, Amblypygi). *J Comp Physiol A* 2009, 195:393–399.
 99. Smith JC, Baker HD. Conditioning in the horseshoe crab. *J Comp Physiol Psychol* 1960, 53:279–281.
 100. Sutherland NS. Visual discrimination of orientation by octopus. *Br J Psychol* 1957, 48:55–71.
 101. Cole PD, Adamo SA. Cuttlefish (*Sepia officinalis*: Cephalopoda) hunting behavior and associative learning. *Anim Cogn* 2005, 8:27–30.
 102. Wen JY, Kumar N, Morrison G, Rambaldini G, Runciman S, Rousseau J, van der Kooy D. Mutations that prevent associative learning in *C. elegans*. *Behav Neurosci* 1997, 111:354–368.
 103. Morrison GE, Wen JY, Runciman S, van der Kooy D. Olfactory associative learning in *Caenorhabditis elegans* is impaired in *lrn-1* and *lrn-2* mutants. *Behav Neurosci* 1999, 113:358–367.
 104. Henderson TB, Strong PN Jr. Classical conditioning in the leech *Macrobdella ditetra* as a function of CS and UCS intensity. *Cond Reflex* 1972, 7: 210–215.
 105. Sahley CL, Boulis NM, Schurman B. Associative learning modifies the shortening reflex in the semi-intact leech *Hirudo medicinalis*: effects of pairing, predictability, and CS preexposure. *Behav Neurosci* 1994, 108:340–346.
 106. Herz MJ, Peeke HVS, Wyers EJ. Classical conditioning of the extension response in the earthworm. *Physiol Behav* 1967, 2:409–411.
 107. Carew TJ, Walters ET, Kandel ER. Classical conditioning in a simple withdrawal reflex in *Aplysia californica*. *J Neurosci* 1981, 1:1426–1437.
 108. Lechner HA, Baxter DA, Byrne JH. Classical conditioning of feeding in *Aplysia*: I. Behavioral analysis. *J Neurosci* 2000, 20:3369–3376.
 109. Kemenes G, Staras K, Benjamin PR. In vitro appetitive classical conditioning of the feeding response in the pond snail *Lymnaea stagnalis*. *J Neurophysiol* 1997, 78:2351–2362.
 110. Sahley C, Rudy JW, Gelperin A. An analysis of associative learning in a terrestrial mollusc. *J Comp Physiol* 1981, 144:1–8.
 111. Thompson R, McConnell J. Classical conditioning in the planarian, *Dugesia dorotocephala*. *J Comp Physiol Psychol* 1955, 48:65–68.
 112. Haralson JV, Groff CI, Haralson SJ. Classical conditioning in the sea anemone, *Cribrina xanthogrammica*. *Physiol Behav* 1975, 15:455–460.
 113. Ferguson HJ, Cobey S, Smith BH. Sensitivity to a change in reward is heritable in the honeybee, *Apis mellifera*. *Anim Behav* 2001, 61:527–534.
 114. Komischke B, Sandoz JC, Lachnit H, Giurfa M. Non-elemental processing in olfactory discrimination tasks needs bilateral input in honeybees. *Behav Brain Res* 2003, 145:135–143.
 115. Longo N. Probability-learning and habit-reversal in the cockroach. *Am J Psychol* 1964, 77:29–41.
 116. Tully T, Quinn WG. Classical conditioning and retention in normal and mutant *Drosophila melanogaster*. *J Comp Physiol A* 1985, 157:263–277.
 117. Schneirla TC. Learning and orientation in ants. *Comp Psychol Monogr* 1929, 6:143.
 118. Kelber A. Colour learning in the hawkmoth *Macroglossum stellatarum*. *J Exp Biol* 1996, 199:1127–1131.
 119. Behmer ST, Belt CE, Shapiro MS. Variable rewards and discrimination ability in an insect herbivore: what and how does a hungry locust learn? *J Exp Biol* 2005, 208:3463–3473.
 120. Weiss MR. Innate colour preferences and flexible colour learning in the pipevine swallowtail. *Anim Behav* 1997, 53:1043–1052.
 121. Datta LE, Milstein S, Bitterman EM. Habit reversal in the crab. *J Comp Physiol Psychol* 1960, 53:275–278.
 122. Capretta PJ, Rea R. Discrimination reversal learning in the crayfish. *Anim Behav* 1967, 15:6–7.
 123. Tomina Y, Takahata M. Discrimination learning with light stimuli in restrained American lobster. *Behav Brain Res* 2012, 229:91–105.
 124. Mackintosh J. An investigation of reversal learning in *Octopus vulgaris* lamarck. *Q J Exp Psychol* 1962, 14:15–22.
 125. Karson MA, Boal JG, Hanlon RT. Experimental evidence for spatial learning in cuttlefish (*Sepia officinalis*). *J Comp Psychol* 2003, 117:149–155.
 126. Datta LG. Learning in the earthworm, *Lumbricus terrestris*. *Am J Psychol* 1962, 75:531–553.
 127. Chandra SBC, Hosler JS, Smith BH. Heritable variation for latent inhibition and its correlation with reversal learning in honeybees (*Apis mellifera*). *J Comp Psychol* 2000, 114:86–97.
 128. Wright GA, Skinner BD, Smith BH. Ability of honeybee, *Apis mellifera*, to detect and discriminate odors of varieties of canola (*Brassica rapa* and *Brassica napus*) and snapdragon flowers (*Antirrhinum majus*). *J Chem Ecol* 2002, 28:721–740.
 129. Wright GA, Lutmerding A, Dudareva N, Smith BH. Intensity and the ratios of compounds in the scent of snapdragon flowers affect scent discrimination by

- honeybees (*Apis mellifera*). *J Comp Physiol A* 2005, 191:105–114.
130. Rankin CH. Context conditioning in habituation in the nematode *Caenorhabditis elegans*. *Behav Neurosci* 2000, 114:496–505.
 131. Lynn SK, Cnaani J, Papaj DR. Peak shift discrimination learning as a mechanism of signal evolution. *Evolution* 2005, 59:1300–1305.
 132. Wright GA, Kottcamp S, Thompson MGA. Generalization mediates sensitivity to complex odor features in the honeybee. *PLoS One* 2008, 3:e1704.
 133. Wright GA, Choudhary AF, Bentley MA. Reward quality influences the development of learned olfactory biases in honeybees. *Proc Biol Sci* 2009, 276:2597–2604.
 134. Leonard AS, Dornhaus A, Papaj DR. Flowers help bees cope with uncertainty: signal detection and the function of floral complexity. *J Exp Biol* 2011, 214:113–121.
 135. Daly K, Chandra S, Durtschi M, Smith BH. The generalization of an olfactory-based conditioned response reveals unique but overlapping odour representations in the moth *Manduca sexta*. *J Exp Biol* 2001, 203:3085–3095.
 136. Kisch J, Erber J. Operant conditioning of antennal movements in the honey bee. *Behav Brain Res* 1999, 99:93–102.
 137. Eisenstein EM, Carlson AD. Leg position learning in the cockroach nerve cord using an analog technique. *Physiol Behav* 1994, 56:687–691.
 138. Brembs B, Heisenberg M. The operant and the classical in conditioned orientation of *Drosophila melanogaster* at the flight simulator. *Learn Mem* 2000, 7:104–115.
 139. Booker R, Quinn WG. Conditioning of leg position in normal and mutant *Drosophila*. *Proc Natl Acad Sci U S A* 1981, 78:3940–3944.
 140. Wustmann G, Rein K, Wolf R, Heisenberg M. A new paradigm for operant conditioning of *Drosophila melanogaster*. *J Comp Physiol A* 1996, 179:429–436.
 141. Cammaerts MC. Operant conditioning in the ant *Myrmica sabuleti*. *Behav Process* 2004, 67:417–425.
 142. Cammaerts M, Rachidi Z. Olfactive conditioning and use of visual and odorous cues for movement in the ant *Myrmica sabuleti* (Hymenoptera: Formicidae). *Myrmecol News* 2009, 12:117–127.
 143. Leadbeater E, Chittka L. Bumble-bees learn the value of social cues through experience. *Biol Lett* 2009, 5:310–312.
 144. Hoyle G, Field LH. Defense posture and leg-position learning in a primitive insect utilize catchlike tension. *J Neurobiol* 1983, 14:285–298.
 145. Sokolowski MBC, Disma G, Abramson CI. A paradigm for operant conditioning in blow flies (*Phormia terrae novae* Robineau-Desvoidy, 1830). *J Exp Anal Behav* 2010, 93:81–89.
 146. Kelber A, Balkenius A, Warrant EJ. Colour vision in diurnal and nocturnal hawkmoths. *Integr Comp Biol* 2003, 43:571–579.
 147. Forman RR. Leg position learning by an insect. I. A heat avoidance learning paradigm. *J Neurobiol* 1984, 15:127–140.
 148. Abramson CI, Feinman RD. Operant punishment of eye elevation in the green crab, *Carcinus maenas*. *Behav Neural Biol* 1987, 48:259–277.
 149. Abramson CI, Feinman RD. Lever-press conditioning in the crab. *Physiol Behav* 1990, 48:267–272.
 150. Stafstrom CE, Gerstein GL. A paradigm for position learning in the crayfish claw. *Brain Res* 1977, 134:185–190.
 151. Olson G, Strandberg R. Instrumental conditioning in crayfish: lever pulling for food. *Soc Neurosci Abstr* 1979, 5:257.
 152. Kawai N, Kono R, Sugimoto S. Avoidance learning in the crayfish (*Procambarus clarkii*) depends on the predatory imminence of the unconditioned stimulus: a behavior systems approach to learning in invertebrates. *Behav Brain Res* 2004, 150:229–237.
 153. Tomina Y, Takahata M. A behavioral analysis of force-controlled operant tasks in American lobster. *Physiol Behav* 2010, 101:108–116.
 154. Papini MR, Bitterman ME. Appetitive conditioning in *Octopus cyanea*. *J Comp Psychol* 1991, 105:107–114.
 155. Crancher P, King MG, Bennett A, Montgomery RB. Conditioning of a free operant in *Octopus cyaneus* Gray. *J Exp Anal Behav* 1972, 17:359–362.
 156. Brembs B. Operant reward learning in *Aplysia*. *Curr Dir Psychol Sci* 2003, 12:218–221.
 157. Lukowiak K, Ringseis E, Spencer G, Wildering W, Syed N. Operant conditioning of aerial respiratory behaviour in *Lymnaea stagnalis*. *J Exp Biol* 1996, 199:683–691.
 158. Kobayashi S, Kojima S, Yamanaka M, Sadamoto H, Nakamura H, Fujito Y, Kawai R, Sakakibara M, Ito E. Operant conditioning of escape behavior in the pond snail, *Lymnaea stagnalis*. *Zool Sci* 1998, 15:683–690.
 159. Mota T, Giurfa M, Sandoz J-C. Color modulates olfactory learning in honeybees by an occasion-setting mechanism. *Learn Mem* 2011, 18:144–155.
 160. Koltermann R. 24-Std-Periodik in der Langzeiterinnerung an Duft- und Farbsignale bei der Honigbiene [Circadian memory rhythm after scent and colour training with honey-bees]. *Z Vergl Physiol* 1971, 75:49–68.
 161. Gould JL. Honey-bees store learned flower-landing behavior according to time of day. *Anim Behav* 1987, 35:1579–1581.
 162. Collett TS, Kelber A. The retrieval of visuo-spatial memories by honeybees. *J Comp Physiol A* 1988, 163:145–150.

163. Schubert M, Lachnit H, Francucci S, Giurfa M. Nonelemental visual learning in honeybees. *Anim Behav* 2002, 64:175–184.
164. Deisig N, Lachnit H, Giurfa M, Hellstern F. Configural olfactory learning in honeybees: negative and positive patterning discrimination. *Learn Mem* 2001, 8:70–78.
165. Sato C, Matsumoto Y, Sakura M, Mizunami M. Contextual olfactory learning in cockroaches. *Neuroreport* 2006, 17:553–557.
166. Brembs BR, Wiener J. Context and occasion setting in *Drosophila* visual learning. *Learn Mem* 2006, 13:618–628.
167. Bos N, Guerrieri FJ, D'ettorre P. Significance of chemical recognition cues is context dependent in ants. *Anim Behav* 2010, 80:839–844.
168. Fauria K, Dale K, Colborn M, Collett TS. Learning speed and contextual isolation in bumblebees. *J Exp Biol* 2002, 205:1009–1018.
169. Matsumoto Y, Mizunami M. Context-dependent olfactory learning in an insect. *Learn Mem* 2004, 11:288–293.
170. Livermore A, Hutson M, Ngo V, Hadjisimos R, Derby CD. Elemental and configural learning and the perception of odorant mixtures by the spiny lobster *Panulirus argus*. *Physiol Behav* 1997, 62:169–174.
171. Gross HJ, Pahl M, Si A, Zhu H, Tautz J, Zhang S. Number-based visual generalisation in the honeybee. *PLoS One* 2009, 4:e4263.
172. Chittka L, Geiger K. Can honey bees count landmarks? *Anim Behav* 1995, 49:159–164.
173. Dacke M, Srinivasan MV. Evidence for counting in insects. *Anim Cogn* 2008, 11:683–689.
174. Carazo P, Font E, Forteza-Behrendt E, Desfilis E. Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate? *Anim Cogn* 2009, 12:463–470.
175. Cheng K. Arthropod navigation: ants, bees, crabs, spiders finding their way. In: Wasserman EA, Zentall TR, eds. *Comparative Cognition: Experimental Explorations of Animal Intelligence*. Oxford: Oxford University Press; 2006, 189–209.
176. Boles LC, Lohmann KJ. True navigation and magnetic maps in spiny lobsters. *Nature* 2003, 421:60–63.
177. Alves C, Boal JG, Dickel L. Short-distance navigation in cephalopods: a review and synthesis. *Cogn Process* 2008, 9:239–247.
178. Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV. The concepts of 'sameness' and 'difference' in an insect. *Nature* 2001, 410:930–933.
179. Avarguès-Weber A, Dyer AG, Giurfa M. Conceptualization of above and below relationships by an insect. *Proc Biol Sci* 2011, 278:898–905.
180. Brown MF, Sayde JM. Same/different discrimination by bumblebee colonies. *Anim Cogn* 2013, 16:117–125.
181. Domjan M. *The Principles of Learning and Behavior*. 5th ed. Belmont, CA: Thomson Wadsworth; 2006.
182. Mallatt J, Craig CW, Yoder MJ. Nearly complete rRNA genes from 371 Animalia: Updated structure-based alignment and detailed phylogenetic analysis. *Mol Phylogenet Evol* 2012, 64:603–617.
183. Giurfa M. Cognition with few neurons: higher-order learning in insects. *Trends Neurosci* 2013, 36:285–294.
184. Thorndike EL. *Animal Intelligence*. New York: Macmillan; 1911.
185. Skinner BF. *The Behavior of Organisms: An Experimental Analysis*. New York: Appleton-Century-Crofts; 1938.
186. Pavlov IP. *Conditioned Reflexes*. Oxford: Oxford University Press; 1927.
187. Kuwabara M. Bildung des bedingten Reflexes von Pavlovs Typus bei der Honigbiene *Apis mellifica*. *J Fac Sci Hokkaido Univ (Ser 6)* 1957, 13:458–464.
188. Bitterman ME, Menzel R, Fietz A, Schäfer S. Classical conditioning of proboscis extension in honeybees *Apis mellifera*. *J Comp Physiol* 1983, 97:107–119.
189. Giurfa M, Sandoz JC. Invertebrate learning and memory: fifty years of olfactory conditioning of the proboscis extension response in honeybees. *Learn Mem* 2012, 19:54–66.
190. McGuire TR. Learning in three species of Diptera: the blow fly *Phormia regina*, the fruit fly *Drosophila melanogaster*, and the house fly *Musca domestica*. *Behav Genet* 1984, 14:479–526.
191. Fresquet N. Effects of aging on the acquisition and extinction of excitatory conditioning in *Drosophila melanogaster*. *Physiol Behav* 1999, 67:205–211.
192. Menzel R. Searching for the memory trace in a mini-brain, the honeybee. *Learn Mem* 2001, 8:53–62.
193. Brembs B. Operant conditioning in invertebrates. *Curr Opin Neurobiol* 2003, 13:710–717.
194. Brembs B, Plendl W. Double dissociation of PKC and AC manipulations on operant and classical learning in *Drosophila*. *Curr Biol* 2008, 18:1168–1171.
195. Brembs B, Lorenzetti FD, Reyes FD, Baxter DA, Byrne JH. Operant reward learning in *Aplysia*: neuronal correlates and mechanisms. *Science* 2002, 296:1706–1709.
196. Lorenzetti FD, Baxter DA, Byrne JH. Molecular mechanisms underlying a cellular analog of operant reward learning. *Neuron* 2008, 59:815–828.
197. Shettleworth SJ. *Cognition, Evolution, and Behavior*. 2nd ed. New York: Oxford University Press; 2010.
198. Tinbergen N. *The Study of Instinct*. New York: Oxford University Press; 1951.
199. von Frisch K. *The Dance Language and Orientation of Honeybees*. Cambridge: Harvard University Press; 1967.

200. Ware R. Computer-aided nerve tracing in the brain of the rotifer *Asplanchna brightwelli*, Ph.D. dissertation. Massachusetts Institute of Technology, 1971.
201. Meinertzhagen IA, Okamura Y. The larval ascidian nervous system: the chordate brain from its small beginnings. *Trends Neurosci* 2001, 24:401–410.
202. Hawkins RD, Kandel ER, Siegelbaum SA. Learning to modulate transmitter release: themes and variations in synaptic plasticity. *Annu Rev Neurosci* 1993, 16:625–665.
203. Castellucci V, Kandel ER. Presynaptic facilitation as a mechanism for behavioral sensitization in *Aplysia*. *Science* 1976, 194:1176–1178.
204. Konorski J, Miller S. On two types of conditioned reflex. *J Gen Psychol* 1937, 16:264–272.
205. Konorski J, Miller S. Further remarks on two types of conditioned reflex. *J Gen Psychol* 1937, 17:405–407.
206. Kaczer L, Maldonado H. Contrasting role of octopamine in appetitive and aversive learning in the crab *Chasmagnathus*. *PLoS One* 2009, 4:e6223.
207. Brembs B. Mushroom bodies regulate habit formation in *Drosophila*. *Curr Biol* 2009, 19:1351–1355.
208. Spence KW. The differential response in animals to stimuli varying within a single dimension. *Psychol Rev* 1937, 44:430–444.
209. Giurfa M. Social learning in insects: a higher order capacity? *Front Behav Neurosci* 2012, 6:57.
210. Le Pelley ME. Metacognitive monkeys or associative animals? Simple reinforcement learning explains uncertainty in nonhuman animals. *J Exp Psychol Learn Mem Cogn* 2012, 38:686–708.
211. Wystrach A, Beugnon G, Cheng K. Ants might use different view-matching strategies on and off the route. *J Exp Biol* 2012, 215:44–55.
212. Cheng K. Arthropod navigation: ants, bees, crabs, spiders finding their way. In: Zentall TR, Wasserman EA, eds. *The Oxford Handbook of Comparative Cognition*. Oxford: Oxford University Press; 2012, 347–365.
213. Collett TS, Collett M. Memory use in insect visual navigation. *Nat Rev Neurosci* 2002, 3:542–552.
214. Wehner R. Desert ant navigation: how miniature brains solve complex tasks. *J Comp Physiol A* 2003, 189:579–588.
215. Wehner R, Srinivasan MV. Path integration in insects. In: Jeffery KJ, ed. *The Neurobiology of Spatial Behaviour*. Oxford: Oxford University Press; 2003, 9–30.
216. Graham P, Cheng K. Ants use the panoramic skyline as a visual cue during navigation. *Curr Biol* 2009, 19:R935–R937.
217. Kohler M, Wehner R. Idiosyncratic route memories in desert ants, *Melophorus bagoti*: how do they interact with path integration vectors? *Neurobiol Learn Mem* 2005, 83:1–12.
218. Wystrach A, Beugnon G, Cheng K. Landmarks or panoramas: what do navigating ants attend to for guidance? *Front Zool* 2011, 8:21.
219. Wehner R, Meier C, Zollikofer C. The ontogeny of foraging behaviour in desert ants, *Cataglyphis fortis*. *Ecol Entomol* 2004, 29:240–250.
220. Zeil J. Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera) I. Description of flight. *J Comp Physiol A* 1993, 172:189–205.
221. Zeil J. Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera) II. Similarities between orientation and return flights and the use of motion parallax. *J Comp Physiol A* 1993, 172:207–222.
222. Menzel R, Greggers U, Smith A, Berger S, Brandt R, Brunke S, Bundrock G, Hulse S, Plumpe T, Schaupp F, et al. Honey bees navigate according to a map-like spatial memory. *Proc Natl Acad Sci U S A* 2005, 102:3040–3045.
223. Cruse H, Wehner R. No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comput Biol* 2011, 7:e1002009.
224. Colborn M, Ahmad-Annuar A, Fauria K, Collett TS. Contextual modulation of visuomotor associations in bumble-bees (*Bombus terrestris*). *Proc R Soc London, Ser B* 1999, 266:2413–2418.
225. Collett TS, Fry S, Wehner R. Sequence learning by honeybees. *J Comp Physiol A* 1993, 172:693–706.
226. Collett TS, Zeil J. Places and landmarks: an arthropod perspective. In: Healy S, ed. *Spatial Representations in Animals*. Oxford; New York: Oxford University Press; 1998, 18–53.
227. Sandoz JC, Galizia CG, Menzel R. Side-specific olfactory conditioning leads to more specific odor representation between sides but not within sides in the honeybee antennal lobes. *Neuroscience* 2003, 120:1137–1148.
228. Benard J, Stach S, Giurfa M. Categorization of visual stimuli in the honeybee *Apis mellifera*. *Anim Cogn* 2006, 9:257–270.
229. Sandoz JC. Behavioral and neurophysiological study of olfactory perception and learning in honeybees. *Front Syst Neurosci* 2011, 5:98.
230. Mobbs PG. The brain of the honeybee *Apis mellifera* I. The connections and spatial organization of the mushroom bodies. *Philos Trans R Soc Lond B* 1982, 298:309–354.
231. Krofczik S, Menzel R, Nawrot MP. Rapid odor processing in the honeybee antennal lobe network. *Front Comput Neurosci* 2009, 2:9.
232. Menzel R, Giurfa M. Cognitive architecture of a mini-brain: the honeybee. *Trends Cogn Sci* 2001, 5:62–71.
233. Galizia CG, Menzel R. The role of glomeruli in the neural representation of odours: results from optical recording studies. *J Insect Physiol* 2001, 47:115–130.

234. Joerges J, Küttner A, Galizia CG, Menzel R. Representations of odours and odour mixtures visualized in the honeybee brain. *Nature* 1997, 387:285–288.
235. Perez-Orive J, Mazor O, Turner GC, Cassenaer S, Wilson RI, Laurent G. Oscillations and sparsening of odor representations in the mushroom body. *Science* 2002, 297:359–365.
236. Turner GC, Bazhenov M, Laurent G. Olfactory representations by *Drosophila* mushroom body neurons. *J Neurophysiol* 2008, 99:734–746.
237. Ito I, Ong RCY, Raman B, Stopfer M. Sparse odor representation and olfactory learning. *Nat Neurosci* 2008, 11:1177–1184.
238. Szyszka P, Ditzen M, Galkin A, Galizia CG, Menzel R. Sparsening and temporal sharpening of olfactory representations in the honeybee mushroom bodies. *J Neurophysiol* 2005, 94:3303–3313.
239. Rybak J, Menzel R. Anatomy of the mushroom bodies in the honey bee brain—the neuronal connections of the alpha-lobe. *J Comp Neurol* 1993, 334:444–465.
240. Strube-Bloss MF, Nawrot MP, Menzel R. Mushroom body output neurons encode odor-reward associations. *J Neurosci* 2012, 31:3129–3140.
241. Huerta R, Nowotny T. Fast and robust learning by reinforcement signals: explorations in the insect brain. *Neural Comput* 2009, 24:2473–2507.
242. Barron AB, Søvik E, Cornish JL. The roles of dopamine and related compounds in reward-seeking behavior across animal phyla. *Front Behav Neurosci* 2010, 4:63.
243. Perry CJ, Barron AB. Neural mechanisms of reward in insects. *Ann Rev Entomol* 2013, 58:543–562.
244. Grünewald B. Morphology of feedback neurons in the mushroom body of the honeybee *Apis mellifera*. *J Comp Neurol* 1999, 404:114–126.
245. Burke CJ, Huetteroth W, Oswald D, Perisse E, Krashes MJ, Das G, Gohl D, Silies M, Certel S, Waddell S. Layered reward signalling through octopamine and dopamine in *Drosophila*. *Nature* 2012, 492:433–437.
246. Cassenaer S, Laurent G. Hebbian STDP in mushroom bodies facilitates the synchronous flow of olfactory information in locusts. *Nature* 2007, 448:709–713.
247. Smith BH, Huerta R, Bazhenov M, Sinakevitch I. Distributed plasticity for olfactory learning and memory in the honey bee brain. In: Galizia GC, Eisenhardt D, Giurfa M, eds. *Honeybee Neurobiology and Behavior*. New York: Springer; 2012, 393–409.
248. Faber T, Joerges J, Menzel R. Associative learning modifies neural representations of odors in the insect brain. *Nat Neurosci* 1999, 2:74–78.
249. Fernandez PC, Locatelli FF, Person-Rennell N, Deleo G, Smith BH. Associative conditioning tunes transient dynamics of early olfactory processing. *J Neurosci* 2009, 29:10191–10202.
250. Abel R. Das olfaktorische System der Honigbiene: electrophysiologische und morphologische Charakterisierung von Entennal-lobus neurones und deren Beteiligung beim olfaktorischen Lernen, Ph.D. dissertation. Freie Universität Berlin, 1997.
251. Szyszka P, Galkin A, Menzel R. Associative and non-associative plasticity in Kenyon cells of the honeybee mushroom body. *Front Syst Neurosci* 2008, 2:3.
252. Mauelshagen J. Neural correlates of olfactory learning paradigms in an identified neuron in the honeybee brain. *J Neurophysiol* 1993, 69:609–625.
253. Okada R, Rybak J, Manz G, Menzel R. Learning-related plasticity in PE1 and other mushroom body-extrinsic neurons in the honeybee brain. *J Neurosci* 2007, 27:11736–11747.
254. Menzel R, Manz G. Neural plasticity of mushroom body-extrinsic neurons in the honeybee brain. *J Exp Biol* 2005, 208:4317–4332.
255. Bazhenov M, Huerta R, Smith B. A computational framework for understanding decision making through integration of basic learning rules. *J Neurosci* 2013, 33:5686–5697.
256. O'Reilly RC. Generalisation in interactive networks: the benefits of inhibitory competition and Hebbian learning. *Neural Comput* 2001, 13:1199–1241.
257. Huerta R, Amigo JM, Nowotny T, Elkan C. Inhibition in multiclass classification. *Neural Comput* 2012, 24:2473–2507.
258. Huerta R. Learning pattern recognition and decision making in the insect brain. *Proceedings of the 12th Granada Seminar on Computational and Statistical Physics*, La Herradura Spain; 2012.
259. Chandra SBC, Wright GA, Smith BH. Latent inhibition in the honey bee, *Apis mellifera*: is it a unitary phenomenon? *Anim Cogn* 2010, 13:805–815.
260. Dacher M, Smith BH. Olfactory interference during inhibitory backward pairing in honey bees. *PLoS One* 2008, 3:e3513.
261. Smith BH, Abramson CI. Conditional withholding of proboscis extension in honeybees (*Apis mellifera*) during discriminative punishment. *J Comp Psychol* 1991, 105:345–356.
262. Wang Y, Dubnau J, Tully T, Zhong Y. Genetics in learning and memory. In: Kesner RP, Martinez JL Jr, eds. *Neurobiology of Learning and Memory*. New York: Academic Press; 2007, 103–127.