

How foresight might support the behavioral flexibility of arthropods

Clint J Perry¹ and Lars Chittka^{1,2}



The small brains of insects and other invertebrates are often thought to constrain these animals to live entirely ‘in the moment’. In this view, each one of their many seemingly hard-wired behavioral routines is triggered by a precisely defined environmental stimulus configuration, but there is no mental appreciation of the possible outcomes of one’s actions, and therefore little flexibility. However, many studies show problem-solving behavior in various arthropod species that falls outside the range of fixed behavior routines. We propose that a basic form of foresight, the ability to predict the outcomes of one’s own actions, is at the heart of such behavioral flexibility, and that the evolutionary roots of such outcome expectation are found in the need to disentangle sensory input that is predictable from self-generated motion versus input generated by changes in the outside world. Based on this, locusts, grasshoppers, dragonflies and flies seem to use internal models of the surrounding world to tailor their actions adaptively to predict the imminent future. Honeybees and orb-weaving spiders appear to act towards a desired outcome of their respective constructions, and the genetically pre-programmed routines that govern these constructions are subordinate to achieving the desired goal. Jumping spiders seem to preplan their route to prey suggesting they recognize the spatial challenge and actions necessary to obtain prey. Bumblebees and ants utilize objects not encountered in the wild as types of tools to solve problems in a manner that suggests an awareness of the desired outcome. Here we speculate that it may be simpler, in terms of the required evolutionary changes, computation and neural architecture, for arthropods to recognize their goal and predict the outcomes of their actions towards that goal, rather than having a large number of pre-programmed behaviors necessary to account for their observed behavioral flexibility.

Addresses

¹ Department of Biological and Experimental Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK

² Wissenschaftskolleg/Institute for Advanced Study, Wallotstrasse 19, 14193 Berlin, Germany

Corresponding author: Perry, Clint J (clint.perry@qmul.ac.uk)

Current Opinion in Neurobiology 2019, **54**:171–177

This review comes from a themed issue on **Neurobiology of learning and plasticity**

Edited by Scott Waddell and Jesper Sjotrom

<https://doi.org/10.1016/j.conb.2018.10.014>

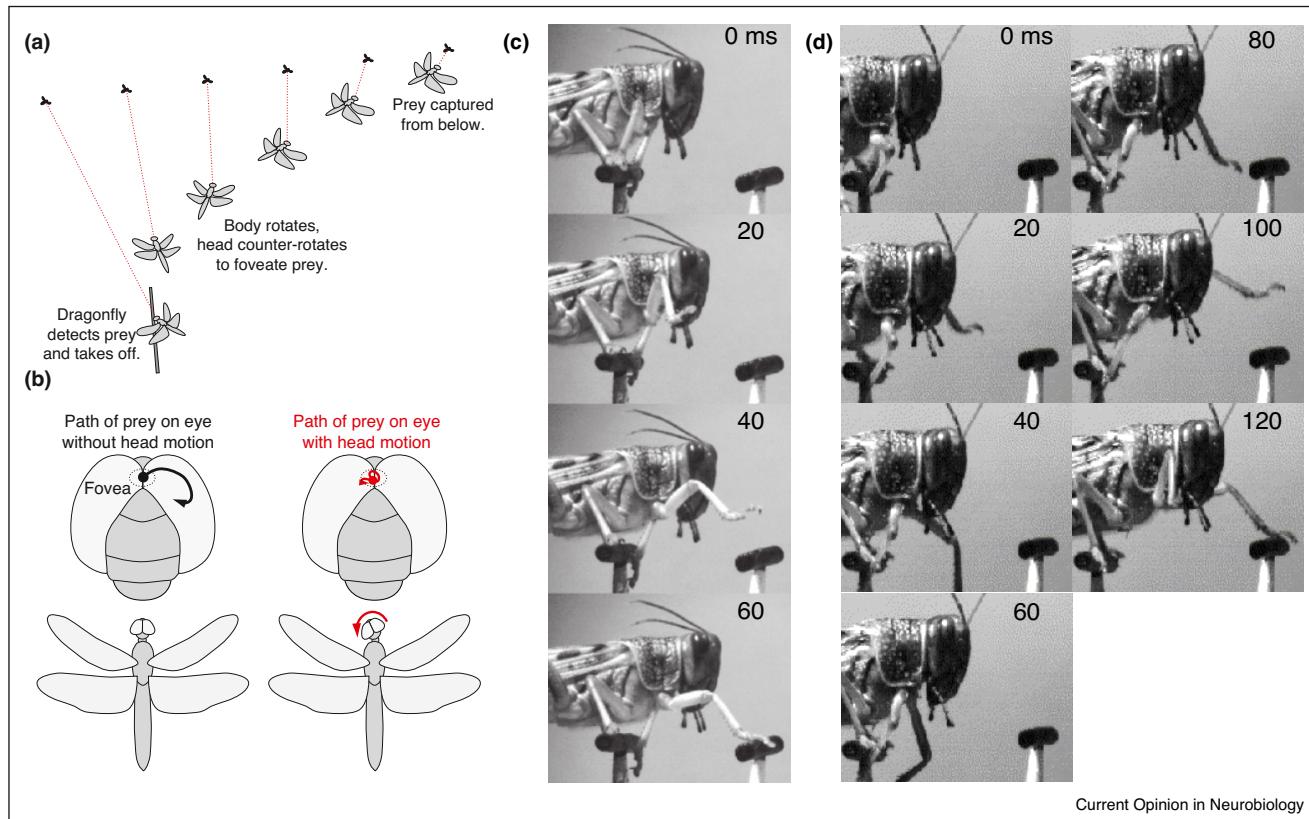
0959-4388/© 2019 Elsevier Ltd. All rights reserved.

Introduction

The diverse types of behaviors in insects and other arthropods (e.g. in nest construction, defense and foraging behavior) have often been argued to be a result of relatively fixed (genetically pre-programmed) routines which require no learning, suggesting that such animals have little behavioral flexibility [1]. We review new literature indicating that arthropods are able to make decisions with a basic recognition of their goals and problems they face. We suspect that such recognition is rooted in the fact that meaningful interpretation of the input from sensors such as image-forming eyes is only possible when one takes into account one’s own intentions to move (or not move) these sensors. Such notions of links between action and perception date back to the 1800’s – for example, Johannes Purkinje’s work (1825) on why active, voluntary movement of the eye does not cause perception of movement of the visual scene, but pressing the eye with a finger does [2]. This ‘efference copy’ [3] phenomenon has been studied neurophysiologically in crustaceans [4] and insects, where its neural underpinnings are now understood in unparalleled detail [5]. Building on such simple forms of predicting the immediate future, we explore cases which seem to us to indicate that behavioral flexibility in arthropods is linked to a prediction of the sensory input as a consequence of their own actions.

Internal models in insects

An example in which animals need to envisage the immediate future is the pursuit and capture of rapidly moving prey. Mischiati *et al.* [6*] analyzed the interception flights of dragonflies hunting flying prey, and discovered that dragonflies do not just passively react to prey movements but steer their flight using a model of both their own position and movement and their prey trajectory, likely constructed from their initial observations (Figure 1a–b). Evidence of an internal model at the neural circuit level has also been shown in fruit flies. Specific optic-flow-processing neurons within the optic lobes of the fly brain were first shown by Kim *et al.* [5] to be actively silenced during voluntary rapid turns in tethered flight in a virtual arena. More recently, Fujiwara *et al.* [7] showed that these neurons encoded unambiguous quantitative information, for example, velocity and direction, about the fly’s walking behavior independently of vision, revealing a circuit for internally monitoring the fly’s voluntary walking movements. These examples highlight an important aspect of internal models whereby the state

Figure 1

Current Opinion in Neurobiology

Evidence of internal models in dragonfly and locust behavior. (a) After detecting prey, a dragonfly begins flight pursuit and quickly adjusts its head position as its body moves in flight to align with the prey. (b) Because the dragonfly rotates its head nearly instantaneously with body flight maneuvers, the image of the prey remains in the high acuity region of the eyes (fovea), suggesting use of predictive model of the prey's trajectory and copy of the dragonfly's own motor commands. (c) A sequence of video images of a locust as it makes a targeted forelimb movement between rungs. (d) A sequence of images of a locust making an error while targeting a rung. The locust undershoots the rung initially and then quickly retargets the correct position. All images are used with permission – (a-b): [57]; (c-d): [11].

of the system should modulate the processing of sensory information. Gorostiza *et al.* [8•] suppressed flies' flight ability (e.g. clipping wings or genetically altering flight muscle contraction) causing changes in their phototactic response to light. Their results indicate that flies may be able to evaluate their own flight ability and use this evaluation to guide subsequent decisions, and suggest that seemingly simple, hard-wired behaviors comprise a decision-making stage comparing the fly's internal state with external information.

Visually targeted limb movement in grasshoppers

A demanding sensori-motor control problem faced by many animals is the visual targeting of limb movements. This requires that the target location is encoded within the animal's visual system which then must be transformed into coordinated activation of motor neurons that result in movement of the limbs appropriately [9]. This allows animals to move their limbs to anywhere in their

visual field that is within reaching range. Insects can use vision to guide their limb placement during walking [10,11] and turning [12]. Niven *et al.* [13] asked whether grasshoppers (*Pseudoprosopia scabra* and *Prosartoria tertiostriata*) are capable of direct, targeted reaching to locations in their visual space. Insects had to reach across a gap to a foothold to continue movement forward. Grasshoppers extended their limb to the next rungs, relying only on their vision to obtain information about rung location. To ensure that gap detection did not trigger a stereotyped motor pattern, experimenters varied the distance between rungs. Grasshoppers were highly accurate in limb placement and did not attempt to reach for rungs that were outside the range of their limbs. In similar experiments, when the rung of a ladder was removed after step initiation, locusts (*Schistocerca gregaria*) reached for the original rung position before readjusting to the new position (Figure 1c–d). This indicates that they were using working memory of information obtained before or early on in step initiation to predict where the rung

would be in the immediate future, and only changed their behavior once an error was detected [11]. These results suggest that locusts had an internal representation predicting the direction towards the target. Related experiments by Strauss and Pichler [14] found that flies showed persistent orientation toward a landmark that disappeared during the fly's approach and later work by Seelig and Jayaraman [15[•]] identified a neural population in the fly central brain that encodes body orientation even when in darkness or standing still, suggesting the presence of an internal representation of the fly's orientation.

Web construction in spiders

Early evidence for behavioral flexibility supported by a form of foresight comes from Swiss naturalist Francois Huber's 200 years-old work [16] on honeybee comb construction. He confronted bees with various challenges while the comb construction was in progress, and found that bees amended their construction in ways that indicated that they were planning ahead (Figure 2a–c). More recent examples come from research on web building spiders [17[•]]. Orb-web spiders are able to match the size and geometry of their web to the available silk supply [18], adjust-specific geometry of their web in low temperatures in order to shorten web building time [19], modify size and stiffness in wind exposed webs [20], and adjust the size and shape of their webs to spatial constraints [19,21]. One of the more intriguing examples of flexibility might be their ability to construct webs even after loss of legs. Observations indicate that between 5% and 40% of adult spiders, depending on species, are found with at least one missing leg. Although juveniles can regenerate a lost leg, in adults, which are unable to molt, regeneration is not possible. The use of all eight legs in orb-web spiders is important for web construction, as all of the legs are normally utilized during web-building [22]. However, Pasquet *et al.* [23] showed that *Zygella x-notata* that have lost one to two legs adjust the construction and geometry of their webs slightly but were functionally no different from those built by intact spiders - no difference in prey capture efficiency, egg sac production or longevity. The function of webs built by spiders missing up to four legs was also not significantly different than those of intact spiders [17[•]]. One possible way of explaining the spiders' performance is to postulate that spiders possess multiple behavioral routines, one for each challenge (i.e. one for constructing webs with all 8 legs, one for 7 legs, etc.). The alternative, which we favor, is that spiders have an expectation of the construction, and the available genetically pre-programmed motor patterns to achieve that construction are flexible and subordinate to the desired outcome.

Route planning in spiders

An example of foresight is planning, behavior done in the service of future needs. There are several observations of the jumping spider *Portia fimbriata* in the wild behaving

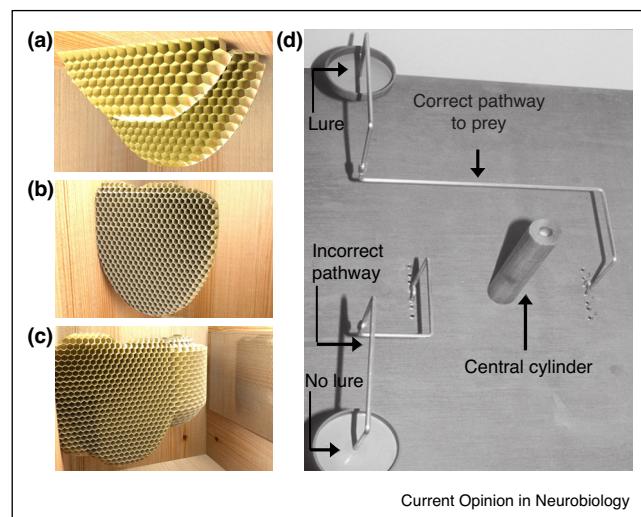
as though it was planning, including detouring away from their prey, in sometimes long and circuitous routes, before heading towards it, appearing to avoid a frontal attack and to surprise the prey [24]. In laboratory experiments, *P. fimbriata* (Figure 2d) were placed on top of a cylinder where they could see two elevated perches, one containing prey (a dead *Eriophora pustulosa* covered in acrylic to avoid olfactory cues) [24,25]. To retrieve the prey, the spider had to descend from the cylinder to the floor, where she could no longer see the prey, and climb an array of poles connected to the prey-containing perch. In a series of different setups, for the spider to reach the prey she had to often walk away from the prey and/or walk past where the incorrect route began. With no prior experience with the setups nor any other sensory information regarding the prey besides seeing it while on the cylinder, spiders chose (contacted the start of a pole array) the correct route significantly more often than the incorrect route, suggesting that these spiders recognized their goal (prey) and the spatial problem they faced (non-straightforward route), envisaged potential actions, and planned their route while atop the cylinder.

Behavioral flexibility through social learning in bumblebees

A recent study explored bumblebees' behavioral flexibility by requiring bees to transport a ball to a defined location in order to receive a reward (sucrose solution) [26]. Bumblebees (*Bombus terrestris*) learned how to solve the task through social demonstration, observing that they could move one of three possible balls (the furthest one from the center) into a central area to obtain reward. When later tested on their own, the observer bees chose not the furthest ball from the center but the closest ball to the center (Figure 3a–b). They did this even when the closest ball was colored black instead of the trained yellow. Importantly, observers had no prior experience with rolling the balls themselves (i.e. no opportunity for operant learning); they also did not simply land near the target area and move the ball that happened to be closest, but instead flew directly to the closest ball after surveying the spatial arrangement. These results indicate that instead of simply copying a learned technique, bumblebees spontaneously improved on the strategy used by the demonstrator, suggesting that they recognized the target of their actions ('ball in goal'), envisioned multiple routes to that target and chose the most efficient one.

Tool use in ants

The above example already indicates a basic form of tool use in an insect, but even more impressive examples of behavioral flexibility can be seen when animals flexibly select the appropriate tools in problem solving. Maák *et al.* [27[•]] investigated tool selection and use in two species of ants (*Aphaenogaster subterranea* and *Aphaenogaster senilis*) by giving them the choice between different types of objects in a foraging situation that required bringing liquid food

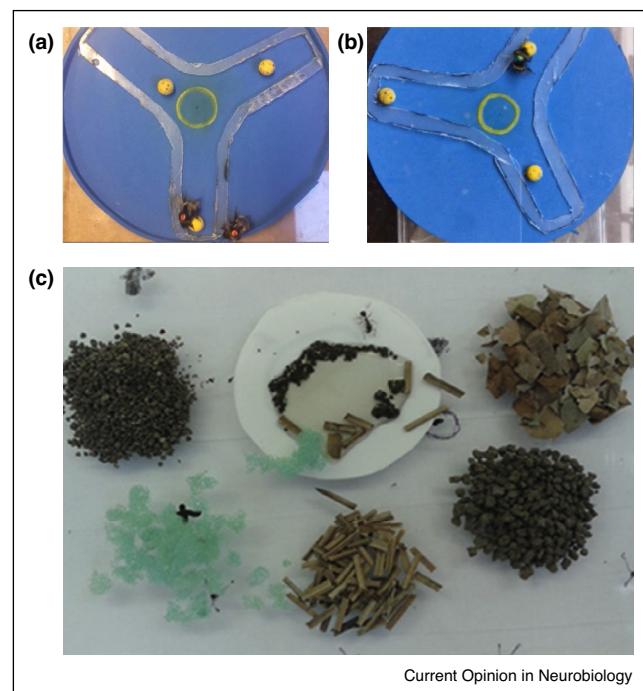
Figure 2

Examples of behavioral flexibility, with possible evidence of planning, in bees and spiders. (a–c) Computer graphic representation of honeybee comb construction in experiments by Huber [58]. (a) Normal construction of multiple parallel combs by cavity nesting honeybees where the comb construction is begun at the ceiling of the cavity. (b) When glass plates were placed on the ceiling and floor, honeybees would begin construction on the side walls. (c) After construction of the comb from one of the side walls had begun, Huber placed a glass plate on the opposite destination wall. Honeybees subsequently, before reaching the opposite wall, curved the construction of the comb 90° to one of the adjacent walls, suggesting that they extrapolated the current direction of the comb wall, deemed it unsuitable and adjusted accordingly. (d) Apparatus for testing planning in spiders. Before each test began, a prey was placed randomly on one of the perches and a jumping spider was placed on top of the central pole. The spider could view the prey from the top of the cylinder, but not when it descended down the cylinder and from the floor. Importantly, the prey was enveloped in acrylic and therefore no other sensory information about the prey was available to the spider other than visual detection while atop the cylinder. The choice of the route that led to the prey suggested the ability to plan ahead. All images used with permission – (a): [16]; (b): [24].

(honey water) back to the nest (Figure 3c). Earlier observations indicated that several ant species use debris to sponge up such liquid food [28–30]. This behavior was flexible in terms of the types of objects ants would choose and utilize for food transport. Ants did not only use objects that they commonly encounter, like soil and twigs, but also objects not available in the wild, such as strings and foam. Impressively, over trials ants preferred to utilize paper or sponge, the most efficient (absorbent) materials available. Ants also cut the sponge into smaller pieces for easier transport. These results show that the ants' ability to use various objects as tools is not rigid and can be flexible in terms of type of objects used and optimal choice of tool with regards to the goal at hand.

The evolution of foresight

One could imagine that arthropods have pre-programmed behavioral routines for each environmental situation they

Figure 3

Tool use and selection in bees and ants. (a) Image from video showing how a bumblebee observed a nestmate rolling the furthest ball from the center of the platform to the center to receive reward. The two balls closer to the center were glued in place. (b) Example of an observer bee during a test alone when all balls could be moved. Note that the bee chose the closest ball from the center to roll, indicating that she recognized the goal at hand, rather than simply copying what she had seen. (c) Different sponging tool types used for the experiment with ants in Maák et al. (2017). From left to right: small soil grains, sponge, pine needles, large soil grains, leaf fragments. Ants learned quickly to use the most efficient tool, sponge, to soak up honey water and transport to their home. All images used with permission – (a): Photos taken by Clint Perry and Olli Loukola; (b): [27].

may come across [31]. But for many species, including those displaying the behavioral flexibility described above, this would likely require an implausibly large number of routines. An extensive array of specialized neural circuits (modules) would presumably be required to solve just the likely challenges. However, this domain-specific tool kit would still not allow an animal to solve novel problems, outside those encountered in their species' evolutionary history. Thus, in addition to postulating even more neural circuits to cope with such challenges, adherents of the neural tool-kit hypothesis would have to explain why arthropods would have evolved specialized mechanisms for scenarios they are unlikely to have encountered before a pesky experimenter ever confronted the animals with them. We therefore favor the notion that at least some arthropods have a more domain-general problem-solving ability, which allows much more behavioral flexibility [32].

The idea of a domain-general problem-solving ability is supported by optimal feedback control theory (OFCT) in relation to motor equivalence (also motor and sensory abundance), the idea that an individual can use a variety of means to towards the same end [33,34]. OFCT suggests that voluntary movement is produced by the central nervous system (CNS) encoding the external goal of the organism within a cost-function and selecting motor commands which minimize this task-dependent cost-function and therefore optimizing behavior [35]. We suggest that more cognition-based tasks may be solved by the CNS through similar methods and functions, comparing internal models of the expected outcome and current state.

Neural circuits allowing for the prediction of the outcome of one's own actions, perceiving desired results and probing for possible paths to achieve them, could provide a selective advantage over fixed behavioral toolkits and would enable an animal to solve novel problems flexibly [36]. We currently have no information about the circuitry that underpins the imagination of possible future states or problem solutions, but we hypothesize that the evolutionary beginnings of such 'forward-planning' circuits may be found in early arthropods with spatially explicit sense organs such as image-forming eyes [37]. Indeed, neurobiological evidence for the 'efference copy' (circuits that allow taking into account the animal's own intentions when interpreting sensory input change), has been found in insects and crustaceans [4,5], suggesting a Cambrian origin of foresight (cf. Ref. [38]).

We've argued so far that foresight (outcome expectation) may explain the above discussed examples of behavioral flexibility in arthropods. It has also been argued that motor control and simple forms of learning (e.g. classical conditioning) are expressed behaviorally as a result of comparing memory with expected outcome [39,40]. Indeed, prediction error learning rules, likely occurring in all animals, are isomorphic to efference copy systems, both relying on the difference between experienced and predicted events for generating a teaching signal and for perception, respectively [39,41]. The fact that these cognitive processes are displayed within such small brains, suggests that outcome expectations might be a fundamental element of cognitive behavior.

Given the similarities between the reward systems of mammals and insects [42], we are inclined to think that the neurobiological underpinnings of outcome expectations would rely on dopamine (and/or octopaminergic) signaling with the mushroom body, high-level sensory integration centers involved in learning and memory [43]. Parallels have been drawn between the reward-predictive properties of (tentatively octopaminergic) VUMmx1 in the honeybee brain and the DA neurons in the mammalian midbrain [41,44]. Further, Schleyer *et al.* [45]

suggested that the outcome expectations found to drive learned behavior in *Drosophila* larvae [40] might come about by a connection from ascending reinforcement processing onto mushroom body output, and such a connection (from dopaminergic mushroom body input neurons onto mushroom body output neurons) was recently identified [46,47].

The circuitry for more advanced planning skills might not be too extensive to accommodate in an arthropod brain either, as shown by neural network architectures that support the outcome predictions of simulated robot actions [48,49]. Recently, Barron & Klein have postulated that the central complex (an evolutionary ancient arthropod brain structure [50]) might support such consciousness-like phenomena, since it is not just crucial for action selection, but also integrates information from the visual periphery, the animal's own motion, its memories and its internal motivational states. Among the insects, however, the most impressive behavioral and cognitive flexibility is found in a few clades of the Hymenoptera that have highly enlarged mushroom bodies, and it is therefore appropriate to explore whether these structures (and their neural circuitry) support the unusual behavioral capacities of these insects. Indeed, even simple models of the bee mushroom body circuit can support relatively complex forms of learning and memory [51–53,54•], but more work is needed to explore how any neural circuit might mediate the elaborate problem-solving skills and prospective cognition observed in these animals. We suspect the spontaneous activities and oscillations reported in various areas of arthropod brains (even in resting states) are at the heart of the mental exploration of possible solutions to complex and unexpected challenges [55,56].

Arthropods, with their relatively compact nervous systems and, in some cases, exceptional behavioral flexibility are tractable systems to determine not only the underlying neural mechanisms of foresight, i.e. outcome expectation, but also the evolution of consciousness-like phenomena in general.

Conflict of interest statement

Nothing declared.

Acknowledgements

This study was supported by HFSP program grant (RGP0022/2014), EPSRC program grant Brains-on-Board (EP/P006094/1), ERC Advanced Grant SpaceRadarPollinator and a Wolfson Royal Society Research Merit Award to Lars Chittka.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest

1. Gould JL, Gould CG: **The insect mind: physics or metaphysics?** *Animal Mind – Human Mind*. Berlin, Heidelberg: Springer; 1982, 269–297.

2. Purkinje J: **Über die Scheinbewegungen, welche im subjectiven.** *Bull. Naturwissenschaftlichen Sect. Schlesischen Ges.* 1825, 4:9-10.
3. Holst E, von und Mittelstaedt H: **Das Reafferenzprinzip.** *Naturwissenschaften* 1950, 37:464-476.
4. Sillar KT, Skorupski P: **Central input to primary afferent neurons in crayfish, *Pacifastacus leniusculus*, is correlated with rhythmic motor output of thoracic ganglia.** *J Neurophysiol* 1986, 55:678-688.
5. Kim AJ et al.: **Cellular evidence for efference copy in *Drosophila* visuomotor processing.** *Nat Neurosci* 2015, 18:1247-1255.
6. Mischianti M et al.: **Internal models direct dragonfly interception steering.** *Nature* 2015, 517:333-338.
Analysis of video-tracking of dragonfly head and body movement during prey pursuit suggest that an internal predictive model of both the prey's trajectory and the dragonfly's own movement is being used in flight.
7. Fujiwara T et al.: **A faithful internal representation of walking movements in the *Drosophila* visual system.** *Nat Neurosci* 2017, 20:72-81.
8. Gorostiza EA et al.: **A decision underlies phototaxis in an insect.**
• *Open Biol* 2016, 6: 160229.
Behavioral tests involving compromising flies' flight ability showed that flies were able to assess their own ability to fly and use this information to modify their behavior with regards to phototaxis, indicating that this traditionally thought innate behavior involves some level of decision making.
9. Shadmehr R et al.: **The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning.** MIT Press; 2005.
10. Pick S, Strauss R: **Goal-driven behavioral adaptations in gap-climbing *Drosophila*.** *Curr Biol* 2005, 15:1473-1478.
11. Niven JE et al.: **Visual targeting of forelimbs in ladder-walking locusts.** *Curr Biol* 2010, 20:86-91.
12. Dürr V, Ebeling W: **The behavioural transition from straight to curve walking: kinetics of leg movement parameters and the initiation of turning.** *J Exp Biol* 2005, 208:2237-2252.
13. Niven JE et al.: **Visually targeted reaching in horse-head grasshoppers.** *Proc Biol Sci* 2012, 279:3697-3705.
14. Strauss R, Pichler J: **Persistence of orientation toward a temporarily invisible landmark in *Drosophila melanogaster*.** *J Comp Physiol A* 1998, 182:411-423.
15. Seelig JD, Jayaraman V: **Neural dynamics for landmark orientation and angular path integration.** *Nature* 2015, 521:186-191.
Two-photon calcium imaging in head-fixed flies walking on a ball in a virtual reality chamber demonstrate that a population of neurons within the center of the fly brain encode the fly's angular orientation, even in darkness or standing still, suggesting the use of an internal model of both environment and their own body movements.
16. Gallo V, Chittka L: **cognitive aspects of comb-building in the honeybee?** *Front Psychol* 2018, 9:900.
17. Hesselberg T: **Exploration behaviour and behavioural flexibility in orb-web spiders: a review.** *Curr Zool* 2015, 61:313-327.
A review discussing orb-web spiders' ability to adapt their webs to space limitations and other environmental disruptions (e.g. wind and temperature fluctuations) and even leg loss, and how these spiders explore their environment and potentially use cognitive maps to solve their web-building problems.
18. Eberhard WG: **Behavioral flexibility in orb web construction: effects of supplies in different silk glands and spider size and weight.** *J Arachnol* 1988, 16:295-302.
19. Vollrath F et al.: **Design variability in web geometry of an orb-weaving spider.** *Physiol Behav* 1997, 62:735-743.
20. Wu C-C et al.: **Wind induces variations in spider web geometry and sticky spiral droplet volume.** *J Exp Biol* 2013, 216:3342-3349.
21. Harmer AMT, Herberstein ME: **Taking it to extremes: what drives extreme web elongation in Australian ladder web spiders (Araneidae: *Telaprocera maudae*)?** *Anim Behav* 2009, 78:499-504.
22. Foelix R: **Biology of Spiders.** USA: Oxford University Press; 2011.
23. Pasquet A et al.: **Loss of legs: is it or not a handicap for an orb-weaving spider?** *Naturwissenschaften* 2011, 98:557.
24. Jackson RR, Cross FR: **Spider cognition.** In *Advances in Insect Physiology*, vol. 41. Edited by Casas J. Academic Press; 2011:115-174.
25. Tarsitano MS, Jackson RR: **Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey.** *Anim Behav* 1997, 53:257-266.
26. Loukola OJ et al.: **Bumblebees show cognitive flexibility by improving on an observed complex behavior.** *Science* 2017, 355:833-836.
27. Maák I et al.: **Tool selection during foraging in two species of funnel ants.** *Anim Behav* 2017, 123:207-216.
Observing the behavior of ants choose different available objects to transport liquid food indicated that their use of tools was not fixed, as their behavior was flexible enough to utilize and even prefer novel objects and to select objects based on their efficiency (soaking properties).
28. Barber JT et al.: **The use of tools for food transportation by the imported fire ant, *Solenopsis invicta*.** *Anim Behav* 1989, 38:550-552.
29. Morrill WL: **Tool using behavior of *Pogonomyrmex badius* (Hymenoptera: Formicidae).** *Fla Entomol* 1972, 55:59-60.
30. McDonald P: **Tool use by the ant, *Novomessor albisetosus* (Mayr).** *J N Y Entomol Soc* 1984, 92:156-161.
31. Perry CJ et al.: **Invertebrate learning and cognition: relating phenomena to neural substrate.** *Wiley Interdiscip Rev Cogn Sci* 2013, 4:561-582.
32. Burkart JM et al.: **The evolution of general intelligence.** *Behav Brain Sci* 2017, 40.
33. Latash ML: **The bliss (not the problem) of motor abundance (not redundancy).** *Exp Brain Res* 2012, 217:1-5.
34. Latash ML: **Synergy.** Oxford University Press; 2008.
35. Todorov E, Jordan MI: **Optimal feedback control as a theory of motor coordination.** *Nat Neurosci* 2002, 5:1226-1235.
36. Suddendorf T, Busby J: **Mental time travel in animals?** *Trends Cogn Sci* 2003, 7:391-396.
37. Godfrey-Smith P: **Other Minds: The Octopus, the sea, and the Deep Origins Of Consciousness.** Farrar, Straus and Giroux; 2016.
38. Bronfman ZZ et al.: **The transition to minimal consciousness through the evolution of associative learning.** *Front Psychol* 2016, 7.
39. Webb B: **Neural mechanisms for prediction: do insects have forward models?** *Trends Neurosci* 2004, 27:278-282.
40. Gerber B, Hendel T: **Outcome expectations drive learned behaviour in larval *Drosophila*.** *Proc R Soc Lond B Biol Sci* 2006, 273:2965-2968.
41. Schultz W: **Predictive reward signal of dopamine neurons.** *J Neurophysiol* 1998, 80:1-27.
42. Perry CJ, Barron AB: **Neural mechanisms of reward in insects.** *Annu Rev Entomol* 2013, 58:543-562.
43. Heisenberg M: **Mushroom body memoir: from maps to models.** *Nat Rev Neurosci* 2003, 4:266-275.
44. Menzel R: **Searching for the memory trace in a mini-brain, the honeybee.** *Learn Mem* 2001, 8:53-62.
45. Schleyer M et al.: **Learning the specific quality of taste reinforcement in larval *Drosophila*.** *eLife* 2015, 4:e04711.
46. Eichler K et al.: **The complete connectome of a learning and memory centre in an insect brain.** *Nature* 2017, 548:175-182.

47. Takemura S-Y et al.: **The comprehensive connectome of a neural substrate for “ON” motion detection in *Drosophila*.** *eLife* 2017, **6**:e24394.
48. Shanahan M: **A cognitive architecture that combines internal simulation with a global workspace.** *Conscious Cogn* 2006, **15**:433-449.
49. Fountas Z, Shanahan M: **A cognitive neural architecture as a robot controller.** *Biomimetic and Biohybrid Systems*. 2013:371-373.
50. Strausfeld NJ, Hirth F: **Deep homology of arthropod central complex and vertebrate basal ganglia.** *Science* 2013, **340**:157-161.
51. Roper M et al.: **Insect bio-inspired neural network provides new evidence on how simple feature detectors can enable complex visual generalization and stimulus location invariance in the miniature brain of honeybees.** *PLOS Comput Biol* 2017, **13**: e1005333.
52. MaBouDi H et al.: **Olfactory learning without the mushroom bodies: spiking neural network models of the honeybee lateral antennal lobe tract reveal its capacities in odour memory tasks of varied complexities.** *PLoS Comput Biol* 2017, **13**: e1005551.
53. Ardin P et al.: **Using an insect mushroom body circuit to encode route memory in complex natural environments.** *PLoS Comput Biol* 2016, **12**:e1004683.
54. Peng F, Chittka L: **A simple computational model of the bee mushroom body can explain seemingly complex forms of olfactory learning and memory.** *Curr Biol* 2017, **27**:224-230.
A simple model based on empirical neurobiological information of the olfactory mushroom body circuitry in the bee brain can explain seemingly complex phenomena such as peak shift and negative and positive patterning discrimination.
55. Yap MHW et al.: **Oscillatory brain activity in spontaneous and induced sleep stages in flies.** *Nat Commun* 2017, **8**:1815.
56. de Bivort BL, van Swinderen B: **Evidence for selective attention in the insect brain.** *Curr Opin Insect Sci* 2016, **15**:9-15.
57. Dickinson MH: **Motor control: how dragonflies catch their prey.** *Curr Biol* 2015, **25**:R232-R234.
58. Huber F: **Nouvelles observations sur les Abeilles, new observations upon bees.** *American Bee Journal*. 2nd edn.. 1814.