The Sensory Ecology of Ant Navigation: From Natural Environments to Neural Mechanisms

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Annu. Rev. Entomol. 2016. 61:63–76

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-010715-023703

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Keywords

navigation, sensory ecology, cue integration, vision, olfaction, multimodal

Abstract

Animals moving through the world are surrounded by potential information. But the components of this rich array that they extract will depend on current behavioral requirements and the animal's own sensory apparatus. Here, we consider the types of information available to social hymenopteran insects, with a specific focus on ants. This topic has a long history and much is known about how ants and other insects use idiothetic information, sky compasses, visual cues, and odor trails. Recent research has highlighted how insects use other sensory information for navigation, such as the olfactory cues provided by the environment. These cues are harder to understand because they submit less easily to anthropomorphic analysis. Here, we take an ecological approach, considering first what information is available to insects, then how different cues might interact, and finally we discuss potential neural correlates of these behaviors.

NAVIGATION BY SINGLE MODALITIES

Animals can use three classes of information for navigation: innate guidance, in which specific motor responses are linked to key cues or signals (46, 94); idiothetic (self-generated) information, which is akin to a human sense of direction (110, 121); and learned information, in which guidance depends on information learned about routes and goals relative to cues from the environment, which may come from a range of sensory modalities (**Figure 1**) (e.g., 13, 15, 18, 98). Studies of these three types of guidance have given us a wealth of information about the sensory basis of navigation.

Visual Cues

Tinbergen (104) famously demonstrated the importance of visual landmarks for insects trying to locate an inconspicuous nest entrance. He placed a ring of pine cones around the nest of a solitary wasp (*Philanthus triangulum*). Upon returning from a foraging journey, the wasp searched for the nest at the center of the ring of pine cones even when the ring had been displaced by the experimenter. These experiments revealed that insects learn something about the landmarks surrounding an important location. Following Tinbergen, experiments with hover flies (*Syritta pipiens*) (24), desert ants (*Cataglyphis bicolor*) (119), honey bees (*Apis mellifera*) (15), water striders (*Gerris paludum*) (55), cockroaches (*Blattella germanica*) (86), crickets (*Gryllus bimaculatus*) (122), and fruit flies (*Drosophila melanogaster*) (80) have all suggested that insects remember the visual information required for navigation to a goal. Remembering the egocentric appearance of the world from a target location is an elegant way for an insect to confirm that it has reached that location. More importantly, an insect can locate a goal by using the discrepancy between its current view of the world and the view of the goal stored in memory, a process called snapshot matching (15, 129).

In addition to learning about discrete locations, many species have solitary foragers that develop idiosyncratic routes that act as proof of individual learning (6, 60). Orchid bees (*Euplusia surinamensis*), for example, use extraordinarily long routes of over 10 km to visit sparsely distributed orchids in a fixed order (54). Compared with those of flying bees, the foraging journeys of walking insects such as ants are much easier to track. Therefore, the habitual foraging route of ants are particularly well-studied [e.g., *Cataglyphis bicolor* (91), *C. fortis* (22), *C. velox* (67), *Paraponera clavata* (5), *Melophorus bagoti* (60), and *Gigantiops destructor* (66)]. Rosengren & Pamilo (89) demonstrated the importance of visual landmarks for navigation along habitual routes by showing that the felling of trees over winter disrupted the ability of wood ant foragers (*Formica rufa* group) to resume their normal routes following hibernation.

The visual systems of insects are very different from those of vertebrates (63), often with eyes of low spatial acuity in the range of 1° to 4° but a near 360° panoramic field of view (**Figure 2**). Here, we do not consider in detail the possible mechanisms by which insects undertake visual navigation with such low resolution, a topic that has been considered in depth elsewhere (20, 128). Rather, we consider in general terms the information that low-resolution vision provides. In the case of an ant forager, its visual system is primarily a navigational sensor because vision is used for few other behaviors. Selection pressure for efficient navigation must have shaped the eye. Evidence from the optical scaling of *C. fortis* workers shows that resolution is often sacrificed for a large field of view (130). The anthropocentric assumption might be that visual navigation requires the identification of specific visual features or objects. However, experiments (39, 40, 126) suggest that navigation is based on the wide-field matching of views and might not require the extraction and identification of landmarks. Matching simple panoramic views rather than isolated landmarks seems an appropriate strategy to cope with the complexity of natural scenes and the poor resolution of insects' eyes (39, 40, 79, 129).

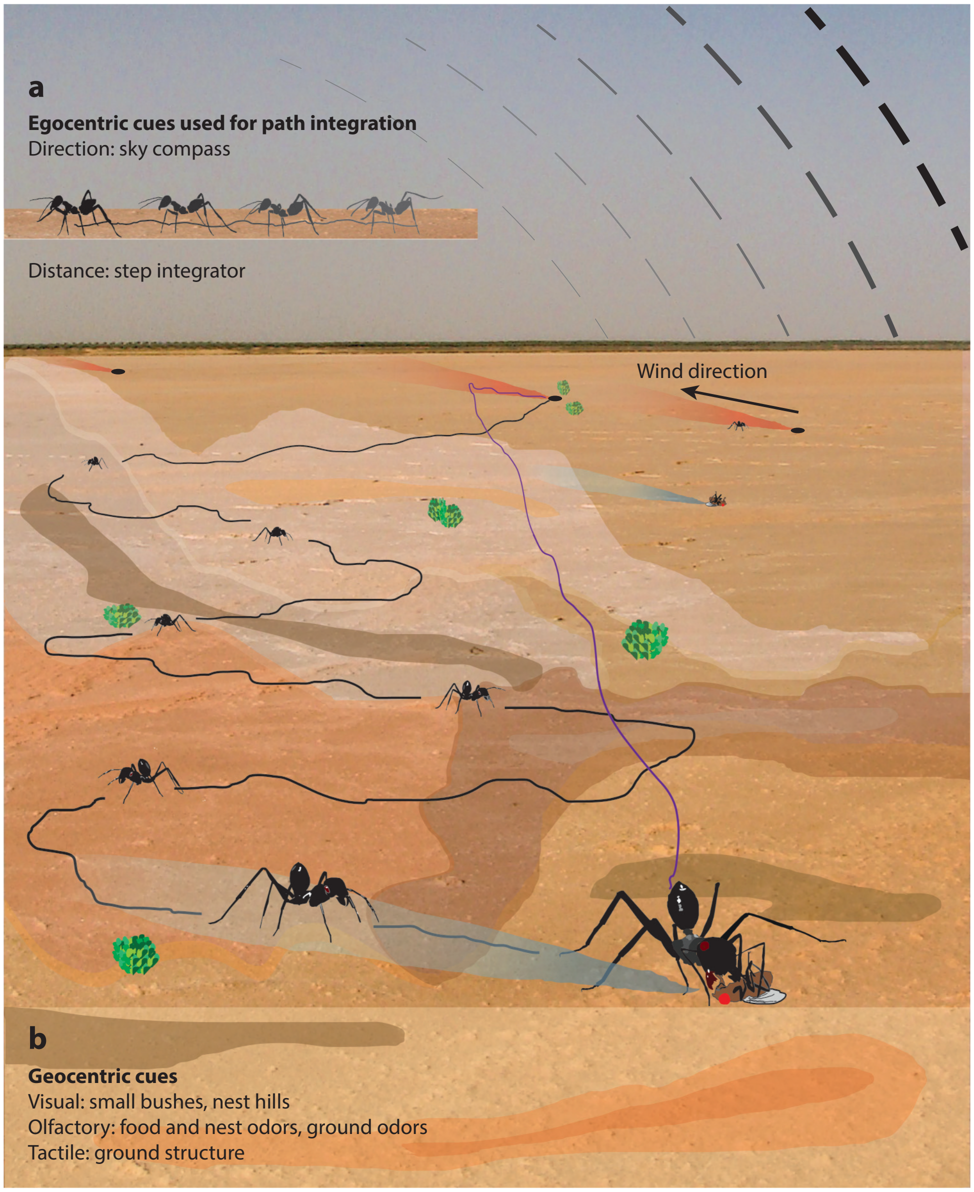

Figure 1

The visual and olfactory navigational toolkit of the desert ant *Cataglyphis fortis*. (*a*) Egocentric cues. The ant uses compass information (from, e.g., a polarized light pattern in the sky, visualized by black bars in top right corner) and distance information from a step integrator to compute its position relative to the nest.
(*b*) Geocentric cues. The ant learns visual cues [e.g., bushes (*green symbols*), stones, and sometimes nest hills] that define the nest entrance or a route. In addition, the ant pinpoints its nest and food items by following odor plumes [red (nest) and blue (food) gradients] and learns place-specific odors en route (*brownish patterns*).

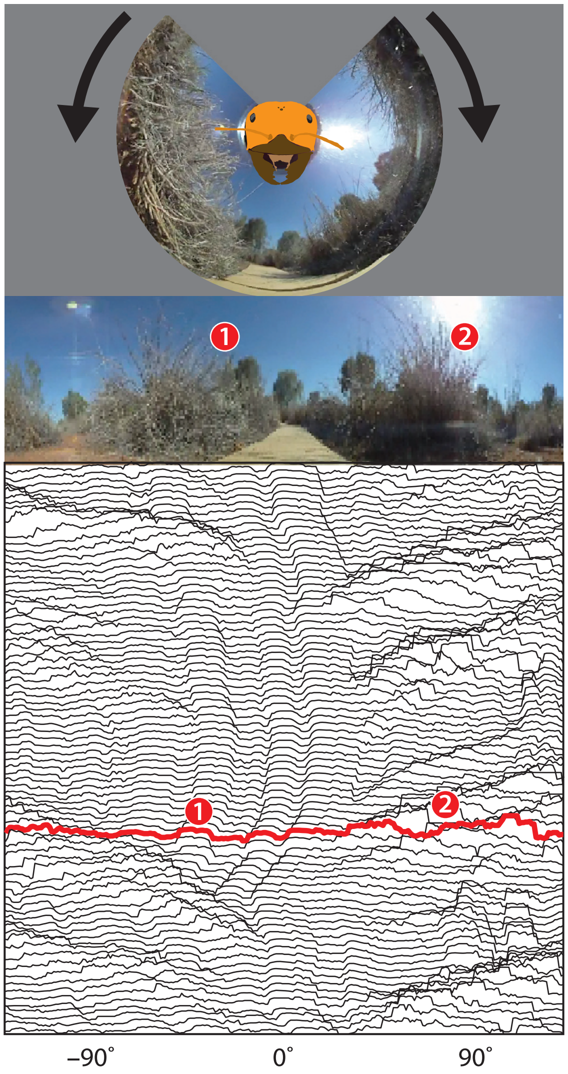

Figure 2

The visual information available to navigating desert ants. The visual field of ants is almost a full hemisphere encompassing the sky and a near panoramic view of terrestrial objects. The low resolution of ant vision, along with the particular spectral tuning of ant photoreceptors, means that the dominant visual features in an ant's eye view of the world will be the high-contrast boundaries between objects and the sky, the skyline. For ants that have developed idiosyncratic routes through cluttered terrain (the figure displays *Melophorus bagoti* and its semiarid habitat in Australia), their visual knowledge of the world resembles a movie, made up of a sequence of skylines that define the appropriate directions to take at different locations along the route. We simulate this by taking a panoramic camera and recording a movie as the camera is moved at ant height along an ant-typical route in the natural habitat of *Melophorus bagoti*. Frames from the movie are unwrapped and trimmed, and the skyline shape is extracted. Features ① and ② of the panoramic view move smoothly in the skyline as the ant progresses along a route.

Low-resolution vision is well-suited to navigation owing to the high information content of low spatial frequencies in natural images (103, 108). Large features in the environment have long been known to influence insect navigation [e.g., mountains (70, 96), forest edges (111)] and may gain their salience by contrasting against the sky and being part of the skyline (35, 37, 39, 61, 73, 105).

The basic properties of natural images, whereby information is available at multiple spatial scales, indicate that the use of stored views for navigation is a robust mechanism. Collett et al. (23) highlight the robustness of using views in this way. They review a series of cases in which the visual knowledge gained by ants during their normal habitual routes can be used to guide them back to a goal or to familiar ground, even from novel locations. A stored view that may be used to guide the animal along a portion of a habitual route contains information about objects at a variety of scales and distances. Even in novel locations, large features that appear in en route views are part of the scene and can often underpin sensible headings for the novel location.

Idiothetic Cues

Central place foragers with no knowledge of their environment must still venture out and try to retrieve food. The mechanism by which many animals do this is path integration (PI). PI involves monitoring the orientation and length of path segments and integrating this information to maintain a continuous estimate of the distance and direction back to the starting point.

Odometric information is provided via either proprioceptive or optic flow mechanisms. For a walking insect that is in contact with the ground, a reliable estimate of distance traveled can be retrieved from monitoring its own leg movements. This step-counting hypothesis was verified for ants by manipulating the leg length before ants were allowed to make a PI-guided return to their nest (123). For flying insects, the influence of wind means that attempts to measure distance in terms of motor output may be inaccurate (32). Rather, flying insects must sense the consequences of their movement, and it has now been shown that a honey bee's estimate of distance depends on the amount of visual motion perceived during a journey (32, 97). Sky cues, such as sun position, polarization patterns created by the scattering of sunlight, and solar chromatic gradients, provide compass information (31, 118). Desert ants also extract compass information from the prevalent wind direction (76), although a role for a magnetic compass cannot be ruled out (113).

PI is an egocentric estimate of position, and so small errors will accumulate throughout a route. Therefore, upon completion of a PI-guided homeward trajectory, the insect may not reach the goal as expected. An inexperienced animal has no choice but to search systematically for the goal (75, 85, 120). These searching behaviors are not simple stereotyped patterns, but rather flexibly controlled depending on the current situation. In general, searches are organized so that the animal spends the most time at the endpoint of their PI home vector and less time at points farther away from this endpoint. However, the spatial extent of the search depends on the expected PI accuracy on the completed journey (51, 71). If we consider PI and search together, then we see that idiothetic strategies guide homing animals such that the length of time they spend at a location is proportional to how likely that location is their goal. Thus, ants produce straight and fast paths far from the nest and they descend into systematic search as they near the goal.

Olfactory Cues

In-depth studies have established olfactory navigation in insects. The pheromone trails of ant species have fascinated people for thousands of years [e.g., Aristotle (3) wrote, "They [ants] come back to their nest by following a rather straight line and on the path they do not hinder one another."] and have become a model behavior for understanding collective behavior and traffic rules

(36). Successful foragers release pheromones on their return to their nest that motivate and guide nestmates to the food source. Pheromone trails may last for months (48, 49, 88) or they may last a short time for the rapid exploitation of a new food source (25). Pheromone communication can even signal unprofitable pathways (87). Whether or not a species uses pheromone trails depends on the distribution of food. Homogenously distributed small food items do not justify pheromone recruitment, as each source will be exploited by the first forager, e.g., individually navigating foragers of the Tunisian desert ant *Cataglyphis fortis*. Habitat temperature seems to be another factor determining whether ants use pheromone trails. In a survey of 50 ant species Ruano et al. (90) found that only those species active at lower temperatures use pheromone trails, probably because higher temperatures decreased trail longevity. However, even at high surface temperatures, ants can use pheromones to recruit and guide nestmates. Scouts of the red harvester ant, *Pogonomyrmex barbatus*, place a specific pheromone drop outside the nest entrance to indicate the direction in which they found food (41). Finally, Namibian desert ants of the species *Ocymyrmex robustior* recruit nestmates with an intermediate strategy. Having found a rich food source (e.g., living termites), foragers return to the nest, recruit a small group of foragers, and lead these foragers to the source by repeatedly touching the gaster to the ground, which most probably releases a volatile pheromone (95).

Although pheromone-trail orientation has been studied extensively, comparatively few studies have investigated the use of other olfactory mechanisms for navigation. Buehlmann et al. (11) showed that *Cataglyphis* ants use odor to pinpoint upwind food sources, i.e., dead insects. The odor of a *Drosophila*-sized insect can attract ants from distances of over 5 m. In addition to pinpointing food, *Cataglyphis* ants use olfaction to pinpoint the nest entrance. During the final portion of their homeward trip, foragers usually pinpoint the nest against the wind, i.e., following a nest-derived plume. One cue driving nest-plume-following behavior is likely to be carbon dioxide (CO_2), which is produced by ants and other organisms (e.g., bacteria, fungi) inhabiting the nest. Indeed, displaced homing ants exposed to an artificial CO_2 plume will follow it as though it originated from a real nest (14). Another study found that *P. barbatus* pinpoints the nest by following olfactory cues (102). Cuticular hydrocarbons [i.e., molecules that are usually responsible for nestmate recognition in hymenopterans (9)] were found to occur in a concentration gradient surrounding the nest entrance. An experiment in which the natural gradient was changed resulted in decreased homing speeds, suggesting that homing ants use this gradient (102). In consideration of both results, it seems reasonable that ants generally use whatever olfactory cue helps pinpoint the nest. Further, Steck et al. (98) showed that *C. fortis* ants can learn to associate artificial odors, which are innately neither attractive nor repulsive, with their nest entrance.

We have outlined above ways in which olfactory cues can be used to guide insects along a trail or to a goal location that is the source of an odorant. One might ask whether at an increased level of sophistication olfaction plays a role in more complex navigation as suggested for pigeons (114, 115). Jacobs (53) even discusses the use of olfactory map-like information as one of the driving forces behind the development of increased olfactory bulb sizes in mammals, for which there is a correlation between the size of the olfactory bulb and an animal's requirements for spatial navigation. Do we see such uses of olfaction in insects? We know that bees can associate multiple feeder locations with different odors. When one of these odors is later blown into the hive, the bees will fly to the (now unscented) feeder, proving that the odor was associated with the navigational instructions required to reach the goal (84). Analogous experiments with *Lasius niger* (26) have reported a similar finding. Wolf & Wehner (124, 125) have shown that, instead of pinpointing a learned feeder directly, experienced *Cataglyphis* ants aim for the expected food plume position. Hence, as for bees, ants incorporate food odors into their navigation.

C. fortis ants also seem able to use olfaction in "proper" navigation (i.e., in a context different from just plume- or trail-following). In addition to nest or food odors, foraging ants are constantly exposed to place-specific odors from the environment. Analyzing 100 odor samples collected from a large grid (100 × 100 m) in the salt pan habitat of *C. fortis*, Buehlmann et al. (12) found several odors with place-specific concentrations, which might therefore provide useful information for guiding the ants along habitual routes (see above). Because place-specific odors cannot be manipulated experimentally, the authors instead trained ants to forage along an alley of artificial odors. When trained ants with no PI information were released in the alley, many of them followed along it (12), unlike naïve ants. Hence, the trained ants did not pinpoint an odor source but remembered a direction associated with a learned odor, similar to experiments in which ants attached so-called local vectors to familiar visual cues (8, 21). On a much smaller scale, the use of olfactory scenes has been previously shown (100). Ants were trained with an array of four different odors (placed at the corner of a square with a side length of 7 cm) surrounding their nest entrance. In tests, ants would focus their nest search at the center of the odor array, but only when all odors were presented in the correct positions, indicative of learning the olfactory scene. Taken together, these results suggest that during navigation ants can use odors in ways more sophisticated than simply pinpointing sources or following trails.

INTEGRATION OF MULTIMODAL INFORMATION

Perhaps the most frequently repeated navigational experiment is performed every summer by people who smear their thumbs over the pheromone trails of ant colonies. The ensuing confusion is short-lived, which suggests cues other than the pheromone trail are also used for navigation. We know that chemicals do not contain polarity information (44, 59, 81), but that trail geometry (52), the direction of laden nestmates (74), visual cues (27, 59), and the celestial compass (4, 47, 116) all contribute to disambiguation of the trail. Hence, the simple behavior of trail-following, which at first glance seems to be purely pheromone driven, turns out to be a task that needs input from additional sensory modalities. Thus, we must view navigation as a multimodal process. Interactions between modalities present challenges and opportunities to a navigating animal. Binding information together can facilitate learning and provide a richer memory of the world, whereas if different modalities indicate different directions, then the individual must arbitrate between them.

Arbitration Between Modalities

Navigation is often the result of arbitration between the outputs of multiple navigation systems, so-called cue integration. Cue integration has been well-studied for vision and PI, for which the long-standing view has been that information provided by visual cues overrides that provided by PI when ants are navigating in familiar, visually informative environments. Evidence for this came from studies of ants' habitual routes, which superficially seem to be unaffected by manipulations to PI (60, 67, 117). However, experiments with more subtle conflict between cues have shown that PI and visual guidance influence the behavior of ants simultaneously (19, 64, 78, 79, 83). This finding raises the fascinating question of whether cue integration is optimized to account for the reliability of different modalities. That is, are directional estimates from a given cue weighted in proportion to the confidence in that estimate (17)? Wystrach et al. (127) have provided the first evidence that ants might be capable of this.

Although nearly all solitary foraging insects are capable of PI and visual guidance, different ant species inhabit environments with different levels of clutter and vegetation; hence, these environments provide different amounts of visual information. **Figures 1** and **2** clearly indicate this for the salt pan and semiarid habitats. Do such differences in visual habitat influence the fine details of cue use and integration? Circumstantial evidence comes from the behavior of different species taken from a familiar feeder and transported to a visually distinctive location. The extent to which they follow the direction indicated by their PI seems to vary as a function of the complexity of their visual environment. *C. fortis* (from the salt pan) will travel almost the entire length of its PI home vector before beginning a search pattern (117). *Gigantiops destructor* from the dense rainforest of South America will travel only a few centimeters in the direction indicated by its PI before beginning a search (7); other species will travel intermediate distances (37, 77). This variation seems to indicate that ants from visually complex environments assign less weight to their PI. However, displacing an ant in a visually complex environment creates a more severe mismatch between the views with which the ant is familiar and the currently perceived scene (16). Buehlmann et al. (10) provide one of the few comparisons that controls for this by using identical experimental setups with different species. Thus, in a comparison of *C. fortis* with *M. bagoti* we can state that *C. fortis* has a more accurate PI system, though the impact of controlled changes to the visual environment were comparable for the two species. These kinds of studies are only beginning to elucidate how cue integration depends on ecology.

Binding of Multimodal Cues

Both vision and olfaction play significant roles in insect navigation, but how do these modalities interact with each other or even synergize? *Drosophila melanogaster* easily learns to associate an olfactory (106) or visual stimulus (29) with either reward or punishment. When trained with a combined visual and olfactory stimulus, *D. melanogaster* displayed facilitated learning of stimuli that were previously shown to be below the detection threshold. These bimodally trained flies then responded to subthreshold stimuli even when presented unimodally in tests (43). Similar results were obtained from honey bees, which after pretraining with a single visual cue later more easily learned the association between an olfactory cue and a sugar reward (38). Bimodal facilitation of learning unimodal cues seems to be a general rule. For instance, human subjects learn to better recognize a human voice when it is presented with a video of the speaking face (112). Also, in a simpler task where subjects had to learn a moving stimulus either in the presence or the absence of an auditory stimulus, bimodal training yielded better results, even in later unimodal (vision only) tests (57, 93).

Similar results are seen when ants are trained to associate their nest entrance with an isolated visual cue, an isolated olfactory cue, or both. Ants learned the component unimodal cues much faster when the cues were presented as a bimodal stimulus rather than as unimodal parts (99). However, after continued training with the bimodal cue, the ants stopped responding to individual cues in a test situation. Hence, although at first the bimodal signal facilitated learning of both modalities, the ants later learned that both signals have to co-occur to be meaningful, suggesting that somewhere in the brain information from different modalities had been merged.

The synergistic effect of two modalities depends on the so-called congruency of cues, especially when the stimulus pairs are ecologically valid; i.e., they naturally occur in the same context. For instance, colors and odors synergize to attract naïve fruit flies but this synergy is restricted to colors and odors from the same fruit source. Colors from, e.g., bayberries do not affect attraction to odors from oranges (34). In another example of two cues in the case of the same modality, the attraction of the nectar-foraging sphingid moth *Manduca sexta* to flower odors of *Datura* or *Nicotiana* was significantly increased in the presence of green leaf odors. However, the synergy was restricted to cases in which flower odors were presented in combination with leaf odors of the same species (56). In summary, animals seem to benefit from the presence of many cues from overlapping or nonoverlapping modalities, especially when the combination is somehow ecologically valid.

How could binding of multimodal cues affect the homing performances of an ant or a foraging bee? Many ants and bees follow idiosyncratic routes (see above). It is therefore imaginable that they repeatedly pass microhabitats with a specific appearance and smell and may incorporate bimodal cues into their knowledge of these routes.

How Does This Play Out in the Brain?

What might be the physiological correlate of the facilitated learning of bimodal cues? Obviously, one modality can influence the other in many ways. Visual neurons in a specific part of the cortex of cats (*Felis silvestris catus*) respond to subthreshold auditory input with increased firing rates (1). Other studies report shortened response latencies within the audio-visual cortex when human subjects were exposed to bimodal instead of unimodal cues (2, 68). Similar results were obtained from experiments with *D. melanogaster*. When recording visually evoked local field potentials (LFPs) within the brains of flies, van Swinderen & Greenspan (107) observed increased LFPs in response to visual stimuli when the flies were also exposed to banana odor. This model organism has only recently become the focus of navigation studies (80), but offers a marvelous genetic toolkit to test for the relevance of individual brain parts for specific behavioral repertories.

Numerous studies on *D. melanogaster* suggest associative olfactory learning occurs in the mushroom bodies (28, 45, 50). Although fruit fly mushroom bodies do not have any direct visual input, a study found distinct but partly overlapping neuronal populations within the mushroom bodies to be involved in both olfactory and visual associative learning (109). Unlike those of *D. melanogaster*, the mushroom bodies of bees (*Bombus impatiens*) and many ant species [as well as *Papilio xuthus* (58) and *Periplaneta americana* (65)] have been shown to receive direct input both from the optical and the antennal lobes (42, 82), and their involvement in visual and olfactory learning and even place learning has been shown both by ablation studies (62, 72, 92) and pharmaceutical blocking of neuronal activity (69). Furthermore, in Hymenoptera the mushroom body collar regions, which are sensitive to visual information, are selectively developed when workers begin their foraging life (30, 101). Finally, Farris (33) found that in insects the capacity for spatial learning is correlated with the evolution of enlarged complex mushroom bodies. Despite the absence of direct evidence, mushroom bodies are hypothesized to be involved in spatial navigation in bees and ants. Mushroom bodies not only process single modalities but are also involved in the integration of olfactory and visual cues, again in support of our main hypothesis that spatial navigation in most insects is based on the integration of input from many sensory modalities.

SUMMARY

Bees and ants have long since been a model for navigation studies. This research started with the investigation of the function and impact of individual modalities, and we now understand that robust navigational performance depends on the use of a wide range of environmental and self-generated information from multiple modalities. Findings from studies on Hymenoptera and *Drosophila* are being examined concomitantly to help us understand the neuronal correlates involved in processing and combining sensory information from different modalities. Future investigations will enable us to understand how these neural mechanisms are tuned to the natural ecology within which animals navigate.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Ralf Möller and Andrew Philippides for comments on the manuscript and Antoine Wystrach for help with **Figure 2**. We also thank Rüdiger Wehner and Tom Collett for introducing us to the study of insect navigation.

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