PNAS COMMENTARY

Toward the vector map in insect navigation

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Navigation is an essential behavior in most animals, necessary to locate food and other resources, to find mates, and to return to shelters or nests. The latter is essential for social insects, such as bees, wasps, and ants. These do not only depend on their nest for survival, they typically also have their queens as the only reproductive individuals. Social insects are highly competent navigators, therefore, rivaling mammals in their performance. Patel et al., in PNAS (1) significantly further our understanding of bees' navigation performance and the underlying mechanisms.

A major navigation strategy of social insects is path integration, the continuous updating of the navigator's position relative to the nest by integrating angles steered and distances traveled by (approximate) vector summation of path increments (2). Path integration allows direct return to the nest from any point during travel and thus is a safe and reliable strategy for homing, even without knowledge of landmarks and other details of the nest surrounds. Vector navigation alone cannot account, however, for more demanding feats like finding novel shortcuts or optimizing travel between series of food sources (3, 4).

In fact, finding novel shortcuts has long been considered the gold standard for proving the existence of a so-called cognitive map in a navigator (4, 5). Such a map, a central representation of the space surrounding an animal, appears as a prerequisite for establishing shortcuts between known locations across unknown terrain.

The use of cognitive maps in mammals is commonly accepted, and the underlying neural substrates and modes of representation are well studied (5, 6). Indeed, map-like representations of space are often considered a privilege of mammals and birds with their comparatively large brains, possessing neuron numbers sufficient to store abundant map details and support population coding of movement in space. The existence of map-like representations in insects has remained controversial, by contrast (4, 7). Small insects are naturally limited in brain size and thus neuron numbers since neurons cannot be miniaturized indefinitely. Insects thus have to make do with relatively few neurons, raising the question of how they achieve behavioral feats rivaling those of mammals.

Patel et al. (1) address exactly these questions: How can (bumble)bees exhibit navigation feats implying the use of a map? What kind of a map may that be, certainly different from the mammalian version? Recent advances in insect neurobiology have revealed much of the central nervous substrates underlying insect path integration (8, 9). These reside in a brain structure termed central complex, common to all insects, and with homologs throughout the arthropods. At the core is a circular network, the so-called central body, a highly ordered structure apparently representing and comparing current and desired locomotor directions by peaks of neuronal activity in the respective central body segments.

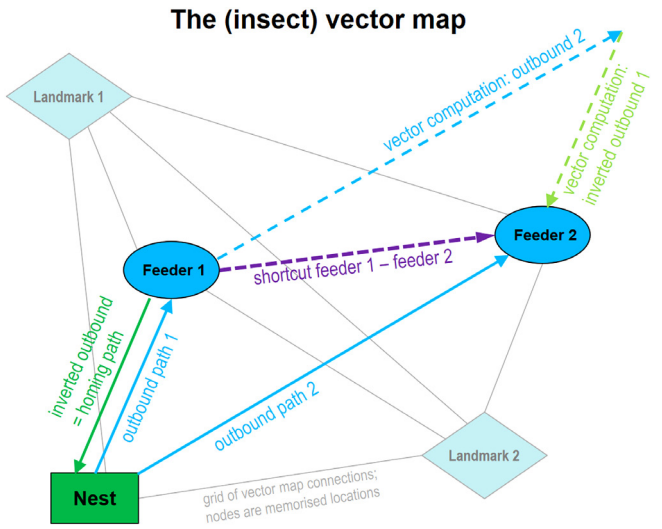

Fig. 1. Schematic diagram, illustrating the presumed insect vector map. Vectors to feeders, blue; homing vector to nest, green; vector addition, broken lines, resulting shortcut vector in violet. Gray lines indicate vectors of the complete map including two landmarks, in addition to feeders and nest.

The path integrator thus appears to reside in the central complex, long known as a center for action selection and steering control (10).

Central complex neuroanatomy is predictive of network connectivity and function, which has stimulated instructive modeling approaches that included both neuroanatomical and behavioral constraints (11). In these models, significant locations such as food sources or landmarks are stored as the associated vectors in (central complex) memory. These vectors are used for both homebound travel after inversion (Fig. 1, green arrow) and for later return to the food source (Fig. 1, blue arrows). Thus, to perform a shortcut between two memorized locations across novel terrain, the navigator simply has to add two vectors (Fig. 1, broken line arrows). This mechanism would produce a decentralized vector map for flexible travel between individually memorized locations, anchored to the real world by the nest location and a grid of nodes of familiar locations. A vector map is a parsimonious solution to the map problem and may explain the navigation

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feats of bees, surprising as they are in these small navigators with limited neuronal resources. The aforementioned neuroanatomy allowed identification of a class of neurons in the central complex (9) suited for long-term storage of navigation vectors. Implementing these neurons in model networks transformed the path integration circuit to a model encoding multiple vectors and using them for vector computations (12). Depending on species, there are roughly one to two dozens of these neurons in a brain hemisphere (9), highlighting the parsimonious character of such a vector map.

Altogether, the neuronal substrates for a vector map in insects have been established and modeling studies are highly suggestive regarding its existence and mode of function. Missing are essential behavioral data that would demonstrate parallel vector memories associated with different locations, which could be combined into a vector map to allow computing of novel trajectories. Patel et al. (1) have addressed exactly that point. Disentangling parallel vector memories in behavioral experiments is no easy matter, though, particularly (short-term) working memory used for path integration during foraging excursions, and long-term memory used to return to familiar food sources. Successful experiments thus require strict constraints to eliminate alternative navigation cues like landmarks.

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In brief, bumblebees had access from their nest to an experimental arena lacking any visual features for orientation, except polarized light illumination from the top. Polarized skylight light is the major compass cue for most insect navigators, and it served the bees as the only directional cue. Previous studies had demonstrated that in this experimental setting (13), the bees perform vector navigation, using the polarized overhead light as compass. In a typical experiment, bees well familiar with the feeder were trapped temporarily right in there and the overhead light polarization turned by 90°. The released bees, having polarized light direction as their only compass cue, homed along paths oriented perpendicular to the nest–feeder axis, that is, in the direction indicated by the (rotated) polarization pattern. This verified the basic orientation strategy, according to many previous insect navigation studies, and it illustrates the paradigm used to answer the above vector memory questions in detail.

1st Question: Is the observed homing path dominated by the working memory from path integration during the current outbound journey? Or is it dominated by the long-term memory established during preceding visits, while becoming familiar with the feeder and its position?

1st Answer. Apparently, bees are guided by a combination of previously established long-term memory and current working memory.

A disagreement between the current home vector from outbound path integration and the home direction in long-term memory (below, 3rd Answer) produced mostly disoriented "homing" paths. However, some paths oriented along a hive–feeder axis in agreement with long-term memory, not the current path integration vector in working memory.

2nd Question. Thus, are bees able to orient without a current path integration vector, exclusively by a vector stored in long-term memory?

2nd Answer. A home vector in long-term memory can be recalled for homing.

Bees without a home vector in working memory were produced by placing them directly in the feeder when they were about to leave the nest, thus precluding outbound path integration. The bumblebees nonetheless exhibited straight homing paths oriented in a direction appropriate for a vector in long-term memory from previous experience.

3rd Question. What are the relative impacts of vectors in working and long-term memory if the two disagree?

3rd Answer. Bees successively shift their initial reliance on long-term memory, when that proves consistently undependable, to the path integration vector in working memory.

A lasting disagreement between long-term and working memory vectors was produced by rotating the polarized overhead illumination by 90° before the bees left the nest to visit the long familiar feeder (virtually shifting feeder position by 90°, compare 1st Answer above). Recording their homing paths during successive foraging bouts then demonstrated the gradual shift in reliance on the two memory types, towards the new vector direction.

4th Question. Do bees learn to disregard erroneous long-term memory and instead rely on path integration vectors in working memory? Or do they transfer working memory to new long-term memory vectors over several consistent foraging trips?

4th Answer. A new long-term memory vector is formed by transfer from working memory, and it coexists with the old long-term memory.

Bees adapted to the new, rotated polarized illumination and lacking an outbound path integration vector (see 2nd Answer) homed according to the situation during the immediately preceding foraging bouts, thus proving the formation of a new long-term memory. Nonetheless, hive locations indicated by the previously used long-term memory were still examined occasionally, demonstrating the coexistence of the two homing vectors in long-term memory.

Patel et al. (1) thus have shown that on the behavioral level, too, all elements exist that are necessary to build a vector map. Namely, i) path integration-derived home vectors can be transferred to long-term memory, ii) at least two such vectors can be stored in parallel, and iii) they can be retrieved at their corresponding familiar locations. Finally, iv) the different vector memories interact flexibly during navigation.

This may end the long-standing debate of map use by social hymenopterans and focus further research on the remaining questions. Although this debate has been fruitful in stimulating creative research, following the path paved by Patel et al. (1) would appear more effective now. A significant sample questions is the concrete organization of novel shortcuts and trap lining on both levels, neuronal substrate and behavior.

The similarities in mammalian and insect navigation strategies appear dictated by ecological necessity. No surprise that comparable navigation feats have evolved in several animal groups, from elephants to social insects. Recent studies in developmental genetics (10) even suggest that the corresponding neural forebrain substrates—vertebrate

(mammalian) basal ganglia and arthropod (insect) central complex—are structures homologous in deep animal phylogeny. Both share many characters ranging from developmental genetics to phylogenomics and neural circuit architecture, and both govern action selection and steering, which appears to have survived divergent evolutionary elaboration over more than 500 My. A sort of vector map may even be at the (developmental) origin of the mammalian central cognitive map. A naive navigator, such as a youngster leaving the den for the first time and in complete ignorance of its surroundings, will have to resort to path integration and landmark learning to build its cognitive map for later in life.

1. R. N. Patel, N. S. Roberts, J. Kempenaers, A. Zadel, S. Heinze, Parallel vector memories in the brain of a bee as foundation for flexible navigation. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2402509121 (2024).
2. M. Müller, R. Wehner, Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. U.S.A.* **85**, 5287–5290 (1988).
3. R. Menzel *et al.*, Honey bees navigate according to a map-like spatial memory. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 3040–3045 (2005).
4. K. Dhein, The cognitive map debate in insects: A historical perspective on what is at stake. *Stud. Hist. Philos. Sci.* **98**, 62–79 (2023).
5. A. T. Bennett, Do animals have cognitive maps? *J. Exp. Biol.* **199**, 219–224 (1996).
6. S. Poulter, T. Hartley, C. Lever, The neurobiology of mammalian navigation. *Curr. Biol.* **28**, R1023–R1042 (2018).
7. R. Wehner, T. Hoinville, H. Cruse, On the 'cognitive map debate' in insect navigation. *Stud. Hist. Philos. Sci.* **102**, 87–89 (2023).
8. B. K. Hulse *et al.*, A connectome of the *Drosophila* central complex reveals network motifs suitable for flexible navigation and context-dependent action selection. *Elife* **10**, e66039 (2021).
9. M. E. Sayre, R. Templin, J. Chavez, J. Kempenaers, S. Heinze, A projectome of the bumblebee central complex. *Elife* **10**, e68911 (2021).
10. N. J. Strausfeld, F. Hirth, Homology versus convergence in resolving transphyletic correspondences of brain organization. *Brain Behav. Evol.* **82**, 215–219 (2013).
11. T. Stone *et al.*, An anatomically constrained model for path integration in the bee brain. *Curr. Biol.* **27**, 3069–3085 (2017).
12. F. Le Moël, T. Stone, M. Lihoreau, A. Wystrach, B. Webb, The central complex as a potential substrate for vector based navigation. *Front. Psychol.* **10**, 690–706 (2019).
13. R. N. Patel, J. Kempenaers, S. Heinze, Vector navigation in walking bumblebees. *Curr. Biol.* **32**, 2871–2883 (2022).