

Neural mechanisms of insect navigation

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We know more about the ethology of insect navigation than the neural substrates. Few studies have shown direct effects of brain manipulation on navigational behaviour; or measure brain responses that clearly relate to the animal's current location or spatial target, independently of specific sensory cues. This is partly due to the methodological problems of obtaining neural data in a naturally behaving animal. However, substantial indirect evidence, such as comparative anatomy and knowledge of the neural circuits that provide relevant sensory inputs provide converging arguments for the role of some specific brain areas: the mushroom bodies; and the central complex. Finally, modelling can help bridge the gap by relating the computational requirements of a given navigational task to the type of computation offered by different brain areas.

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Introduction

Many insects are highly capable navigators, with abilities that rival those of mammals and other vertebrates. This includes long range migration, for example, 3600 km for Monarch butterflies [1], but has been studied in most detail in the context of central place foraging, where the ability to relocate the nest is crucial for the survival of the individual, and efficient relocation of exploitable food sources crucial for the colony. For example, thermophilic desert ants can travel hundreds of metres [2,3] during foraging trips and return directly, with surprising accuracy, to their nest entrance when food is found. Some species perform this in extremely barren areas with few cues, primarily exploiting celestial information for path integration [4]. Others forage in highly cluttered vegetation using visual scene memory [5]. Bees — can develop

efficient trapline routes around multiple food sources [6], and can communicate navigational information about discovered food sources or new nest locations to their hive-mates [7,8]. Foragers of social hymenoptera are also known to successfully return home from novel locations after passive displacement [9], even up to several kilometres in wasps [10,11] and bees [12,13]. Most insect species show rapid learning of navigational cues. In the laboratory, cockroaches learn mazes [14] and cockroaches [15], crickets [16] and fruit-flies [17], can be rapidly trained in place learning tasks, such as the 'hot tin roof' paradigm that parallels the Morris water maze used for rodents [18].

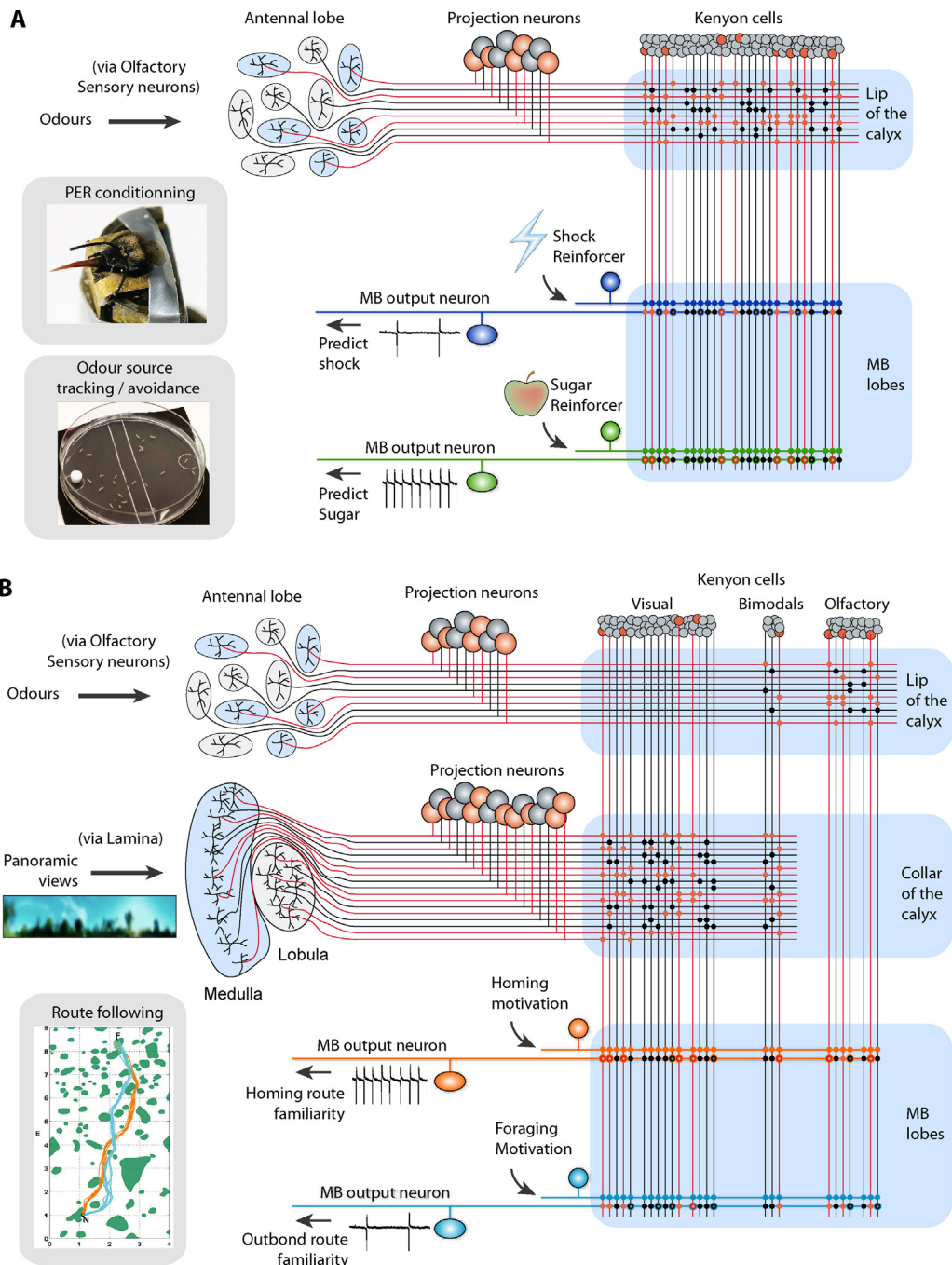
Many years of study have led to a rich understanding of the ecology and mechanisms of insect navigation, especially their capacities for path integration and use of visual memory of their surroundings to follow familiar routes and return to a goal location. However, there is little direct information about the neural substrates of these complex behaviours, for example, no discovered equivalents of the rodent 'place' and 'grid' cells [19]. Indirect evidence comes from first — comparative anatomy of species with different navigational ecologies, second — study of the neural circuits for more basic sensorimotor capacities needed to support navigation and third — computational modelling that demonstrates the plausibility of hypothesised circuits to support the navigational task at hand. Our review raises the question of whether it makes sense to look for the 'navigation circuits' in the insect brain, or whether a better understanding may be obtained by considering how insects weave together a range of general sensory, motor and information processing circuits to support specific navigational tasks.

Direct evidence Manipulation

The clearest form of evidence for the involvement of a brain area or circuit in insect navigation would be demonstration of specific disruption of a navigational behaviour through targeted manipulation of neural activity, comparable, for example, to the loss of maze solving abilities associated with hippocampal lesions in vertebrates [20]. In fact, there are only a handful of studies that provide such direct evidence.

An early study in ants by Vowles [21] used direct lesions (made with a sliver of razor blade) to optic ganglia, the mushroom body (MB, [Figure 1](#)), or the tracts from optic ganglia to MB calyx, and looked at the effects on behaviour in a T-maze task. The clearest effects were seen for lesions of the tract between optic ganglia and MB, whereas lesions

Figure 1



Computation in the Mushroom body can serve various behavioural tasks. **(a)** [Figure modified with permission from [60]]. Circuitry of the mushroom body (MB) is well suited for the storage of a large number of olfactory patterns of activation from the antennal lobe (AL — blue: active; grey: inactive) Each projection neuron (PN) samples one or few glomeruli in the AL and synapses onto multiple Kenyon cells (KC — red: active; black: inactive) in the lip of the MB calyx. Each KC receives input from multiple PNs and thus acts as a coincidence detector, responding only to specific patterns of activation in the AL. Given the impressive number of KCs (e.g., 2000 in flies; 200,000 in bees), the combinatorial number of possible patterns of KC activation is huge, and each will be specific to the perception of a particular bouquet of odour. All KCs then synapse onto a few MB output neurons (MBOs), each being associated with a particular reinforcer neuron in the MB lobes. The coincidental activation of a reinforcer neuron, due for instance to the presence of an unconditioned stimulus (US) like sugar (green), triggers the synaptic modulation of the active KCs output to this MBO. As a result, the MBO will respond only to the specific patterns of odour that have been perceived simultaneously with sugar, even if sugar is no longer present. Several other MBOs could respond to pattern of odour associated to other type of US, such as quinine (not shown) or electrical shock (e.g., in blue). It should be noted that such associative learning may be mediated by KC-MBO decrease rather than increase in synaptic strength [159]. As a result, each MBO carries information about a specific value associated to

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