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Abstract

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 importance 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.

Highlights

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- Visual and multimodal memory of locations could be stored in the mushroom bodies
- Central complex provides aspatial reference frame for integration of directional cues
- Converging evidence suggests the central complex also subserves path integration
- Specific navigational tasks could co-opt circuits with different computational functions
- New methods may be needed to provide direct evidence for functional roles

Introduction

Many insects are highly capable navigators, with abilities that rival those of mammals and other vertebrates. This includes long range migration, e.g., 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 forage kilometres from home (e.g., more than 20 km in orchid bees [6]), can develop efficient trapline routes around multiple food sources [7], and can communicate navigational information about discovered food sources or new nest locations to their hive-mates [8,9]. Foragers of social hymenoptera are also known to successfully return home from novel locations after passive displacement [10], even up to several kilometres in wasps [11,12] and bees [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, e.g., no discovered equivalents of the rodent 'place' and 'grid' cells [19]. Indirect evidence comes from 1-comparative anatomy of species with different navigational ecologies, 2-study of the neural circuits for more basic sensorimotor capacities needed to support navigation and 3-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 byVowles [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 within the MB themselves did not affect performance. We could discover no reported subsequent experiments along these lines for ants, bees or wasps: that is, no direct test of the effect of any form of brain lesion or ablation on their navigation capacities.

The next attempt to ablate MB and look for a navigational deficit used the cockroach [15]. The task involves a circular arena with a hot floor, with one small section held at a lower temperature. Cockroaches can learn to use surrounding visual cues on the walls of the arena to find this safe location. Bilateral lesions of the MB, made by implanting slivers of aluminium foil, disrupted learning for surrounding cues but not for a direct visual cue. Note this 'place learning' capacity does not necessarily require an internal representation of the spatial layout. The same task can be performed by crickets [16], and the behaviour could be successfully modelled [22] by assuming they stored a panoramic view from the safe location, and when placed again at some arbitrary point in the arena, would move so as to reduce the difference between the current and the stored view. In essence, this constitutes performing 'taxis' down a sensory gradient of similarity [23].

It is well established in field experiments in ants and bees that they can use surrounding visual cues to return to the nest after displacement in arbitrary directions [13,24–26]. The demonstration that the cockroach paradigm could also be used in Drosophila [17,27] enabled the use of more sophisticated genetic methods to test the role of specific groups of neurons [28]. This did not reveal any effect of manipulation of MB circuits, but instead suggested a critical role for the central complex (CX, Figure 2); specifically in the R1 neurons of the ellipsoid body. This difference could be due to methodology, or to a real difference between species in how apparently similar stimuli (visual surroundings) and behavioural responses (movement to a goal location relative to visual surroundings) are processed in the brain, as we will discuss further below.

Several other spatial memory tasks in flies also appear to show significant dependence on the CX, and not on the MB. Flies attracted to a vertical bar, but then 'distracted' by a displaced bar, will revert to the original orientation when the bar disappears (Figure 2B), suggesting some form of short term memory for the location of attractive objects. This is affected by manipulating specific CX neurons, in the ellipsoid body [29,30]. However, in a memory task in which heat punishment

occurs in one end of a small arena, rescue of spatial learning in rutabaga mutants occurred for expression of the rutabaga gene in either MB lobes or CX ellipsoid body, but no specific subset of neurons was labelled by all the rescue lines in these two areas; instead, the expression overlap identified antennal lobe, median bundle and ventral ganglia as candidates for rutabaga-dependent place memory [31,32].

More generally, the ability to control oriented action is a necessary component of navigation, and this also points towards a role for the CX [33]. CX disruption in flies has been implicated in a number of directional motor defects, including defects in straight walking, gap crossing, and block climbing [34], and increased centraphobic behaviour [35]. In cockroaches, damage to the CX produces abnormal turning behaviour in response to antennal stimuli [36,37], and optomotor stimuli [38]. Extracellular recordings from the CX in cockroaches on a treadmill have shown responses predictive of turning direction [39]. However some of these oriented behaviours have also been linked to the MB. For example, centrophobism/thigmotaxis is diminished in flies with hydroxyurea ablated MBs [40] with the effect localised through neurogenetic manipulation to the gamma lobe.

The reproductive cycle of the 'classic' insect navigators, bees and ants, does not lend itself easily to deployment of the neurogenetic tools for activation and inactivation of specific subsets of neurons that have been so useful in the fruit-fly, although new methods such as CRISPR [41,42] may open new opportunities. Nevertheless, it seems likely that a mixture of experiments in traditional genetic organisms and the use of alternative brain manipulation methods such as lesions or microinjections [43,44] in bees and ants may continue to be the main avenues of research.

Activity recording

Complementary to direct neural manipulation is the recording of neural activity. Although less clear-cut for causality, measurement of neural activity that is closely correlated to the spatial position of the animal or its current navigation behaviour or target could provide significant insight. The classic example in vertebrates is the 'place cell' [45]. The most relevant evidence is where two or more different sources of input about a navigational cue can independently drive the same neural response , e.g. head direction cells that are influenced by visual cues but still updated by integration of proprioceptive cues in absence of vision [46].

By this criterion there appears to be only one, very recent, example in insects. Seelig and Jayaraman [47], using calcium imaging in a fly walking on a trackball with visual feedback, found that a neural population whose dendrites tile around the ellipsoid body in the CX show activity that tracks the fly's heading as it walks. The neuron population responds to apparent motion of visual cues as well as self-motion cues, and, in the absence of both cues, maintains information about current heading by persistent activity. The response is strongly reminiscent of 'ring attractor' models [48] of head

direction cells, with a moving bump of activity that is not tied to a retinal projection but consistently tracks changes in orientation.

Using a closed loop trackball or flight simulator has a long history in studies of insect sensorimotor control [49,50], including during neural recording [36,51]. However, the provision of a sufficiently complex and complete sensory experience to induce naturalistic navigation behaviour is difficult. A compromise method is to use replay paradigms in which the location and orientation of a freely moving animal is tracked, and the resulting visual experience is reconstructed and played back to a restricted animal while recording neural activity. For example the visual input from learning flights to a feeder has been used as the stimulus in recordings from the bumblebee visual motion pathway in [52]. Advances in mapping natural environments [53] can make such replay highly naturalistic. However, it seems unlikely that such an open loop stimulus will fully engage the animal's own spatial processing system when it is not moving. A second possibility is to exploit and further develop methods for recording neural activity in a freely behaving animal [54–56], especially as improved data analysis methods are increasing the potential information that can be obtained from extracellular probes [57]. However the small size of insects – and the potentially long range of navigation behaviour - poses significant challenges. One option would be to target a larger walking insect that shows some interesting navigational capabilities, such as the dung beetle [58].

Indirect evidence

Brain differences related to navigational capability

One reason that the ablation studies described above focussed on the mushroom body is the longstanding suggestion that the MBs are involved in more 'cognitive' functions, perhaps linked to more complex social organisation [59]; and the substantial evidence that the MB is involved in memory, at least for olfactory associative learning tasks [60]. An early study [61] reported direct correlation of size of MB calyx with individual foraging efficiency of red wood ants in a maze. It has been widely noted that many insects with conspicuous navigational abilities have substantially more complex MBs both in size and structure of the input areasFarris and Schulmeister [62] review this evidence over a range of species and evolutionary history and conclude that MB expansion was rather driven by parasoitidism and generalist scavenging, which require navigational skills, rather than eusociality.

In particular, visual input to the MB is more extensive in insects such as bees [63] and wasps [64] that use vision for navigation than in Drosophila, for example. Ant species relying mainly on chemical cues receive mainly olfactory input to their MB calyces, while ants using vision for navigation receive larger visual input into the MB [65] and have relatively larger visual lobes and eyes [66]. In whirligig beetles, there has been complete change from olfactory to visual input to the

MB, and it has been noted they appear to use visual memory to maintain a stable location in territorial behaviour [67]. In butterflies, substantial differences in the size of MB between species has been related to complexity of their foraging behaviour [68]. Multimodal (olfactory and visual) inputs to the MB have been observed in butterflies [69] and moths [70].

The response properties of MB neurons to visual stimuli has received far less study than their olfactory responses. However, in bees, it seems clear that MB calyx receive a large array of specific visual features from the medulla and lobula, such as wide field or small field chromatic or motion information, as well as temporal features mediated by habituation or 'entrainment' of the projection neurons [71]. Such visual pre-processing may break retinotopy but extract environmental features that facilitate foraging tasks such as the recognition of the locations perceived along a route or in front of a patch of flower.

Within social insects species, changeses over the lifespan of the individual in MB volume and structure can be related to the foraging task (ants: [65,72]; bees:[73–75]; wasps [76]). In desert ants, this change involves both axonal pruning and dendritic growth in the calyx; and can be triggered by exposure to light [77]. It is assumed that such an expansion is due to the increased memory demands in foraging compared to other tasks – either to recall routes, or recognise multimodal cues that signal good food sources, or both. However it may be overly simplistic to equate size to memory capacity.

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To date, there has been no equivalent systematic attempt to relate other insect brain area differences to navigational capabilities. CX elaboration has been associated with goal directed walking and other dextrous limb control [33], and more recently with action selection [78]. Yet, CX neural types and connectivity appear strongly conserved over species with different navigational lifestyles [79], from locusts and dung beetles performing simple polarotaxis, to bees known to perform accurate path integration. However there may be plasticity or tuning of the inputs: a recent study reports an increase in giant synapses conveying polarized light information to the CX in foraging vs. nest-working Cataglyphis ants, which is explicitly triggered by exposure to UV light [80] and may reflect a calibration process for the polarisation compass. Similar specialisation to detect CO_2 signals from the nest entrance [81] or necromone linoleic acid from corpses of dead arthropods [82] might explain enlarged glomeruli observed in the antennal lobe of Cataglyphis ants [83].

Neural circuits for relevant underlying capabilities

Another way to approach the identification of relevant brain circuits for navigation is to consider

specific processing pathways likely to play a key role, as the information they provide – such as distance and direction – is essential to the insect's navigational prowess.

Accurate directional information is crucial to successful navigation, particularly for robust path integration [84], so the rapidly increasing knowledge of the polarised skylight processing pathway in the insect brain is significant (reviewed in [79,85]). Polarised skylight provides an external compass cue, available across a wide part of the upper visual field, and hence rarely fully occluded. Early behavioural studies established that ants and bees use this cue in path integration [8,86] and many other insects use it for directional stabilisation (e.g. crickets: [87]; locusts: [88]; fruitfly: [89,90] Dung beetle: [91]). The criticality of directional information, for example the need for an external compass to make consistent progress away from a starting point [92], suggests this system may be ancient, and although the majority of research comes from the locust, the pathway appears strongly conserved across insects, including long range navigators such as the monarch butterfly, and central place foragers such as bees [79].   The POL-pathway connects specialised receptors in the dorsal rim of the insect eye [93], via segregated areas of the optic lobes, the anterior optic tubercle and the lateral accessory lobe, to the central complex. Within the CX, many neurons show tuning to particular directions of linear polarisation, for example, a regular pattern of preferred e-vector tuning is found across neurons in the protocerebral bridge [94]. The responsiveness of some classes of these neurons to spectral cues and the azimuth or elevation of a light point representing sun position (reviewed in [95]) suggests additional celestial compass information is gathered in CX circuits, and clock cues [96] allow time compensation to make this potentially a true compass.

Path integration also requires information about distance or speed of travel. Famously, this is provided by optic flow in bees [97] ; and 'step counting' in ants [98]; although behavioural studies depict rather complex and multimodal processing of odometric information. For instance, ventral optic flow also plays a role in ants [99] and bees appear to 'count landmarks' [100–102]. Similarly, whether self-motion cues (such as step counting) are tracked by proprioceptive sensing or involve efference copy remains unclear. It has been suggested that we are "completely in the dark" as to how the distance signal for path integration is computed [103], but tracing the neural circuits for the sensory processing of these distance cues seems a promising direction. For optic flow, there is a rich understanding of the visual processing (reviewed in [104,105]) but this is generally in the context of reflexive visual stabilisation [106]. As a substrate for path integration, different constraints on the processing become important, for example, extracting speed independent of the contrast, and the accuracy of the speed information to be integrated [107,108]. It is clearly interesting in this regard to find CX neurons responsive to optic flow [38,109] providing convergence with the key directional information for path integration. Alternatively, if distance input is from proprioception

or efference copy, this still points to a role for the CX - as it shows responses to mechanical stimuli [110] and walking speed [36] in the cockroach. On the other hand, the lobes of the MB also respond to proprioceptive cues such as limb movement [111] and have been linked to predicting (or receiving efference copy of) motor output [112]. An interesting open question is how a neural system can perform the requisite gradual accumulation of velocity over time. Neural integration of a sensory signal can be modelled using recurrent networks [113] or even single neuron properties [114].

Navigation almost certainly requires multimodal integration, and the convergence of celestial compass information, terrestrial information such as visual , wind or chemosensory input and self motion cues such as mechanosensory input led to the suggestion that the CX serves the integration of different spatial frames of reference into a unified representation [115,116]. The anatomy and link to descending units make the CX an ideal candidate for the azimuthal integration of multiple directional cues into a final decision (Figure 2). For instance, when path integration and terrestrial cues indicate two different directions, ants are known to systematically head in-between [25,117–120] and the conflicting cues can be weighted according to their respective reliability [118,119]. Such weighted integration can be effectively achieved by ring attractor neural models [121], but whether and how it is achieved by the CX remains unresolved. The MB also receive multimodal input: to the calyx from different sensory pathways and from protocerebral neuropils; but also to the lobes including proprioceptive cues [122,123]. We can speculate that this enables contextual effects on MB processing of sensory information, but the link between MB and motor control appears less direct than for the CX and remains poorly understood.

Brain circuits shown through computational modelling to have the potential to support navigation

A complementary approach to the data described above is to investigate through computational modelling whether, in principle, particular neural circuits in the insect brain could carry out the functions needed for a navigational task. Although there is an extensive history of modelling in insect navigation, most approaches are at the algorithmic level. Some algorithms have been expressed in neuron-like processing units but with somewhat arbitrary architectures rather than based directly on known anatomy [124–126]; more detailed models of relevant brain areas have been developed but for simpler tasks than navigation, e.g. [127].

Our current modelling work seeks to verify direct connections between neural circuits and navigational capability in insects. We have adapted a model of the MB that was developed to account for Drosophila olfactory conditioning [128] to instead support visual memory in the context of ant route following (figure 2B). Both problems can be seen as the need to store multiple,

differing patterns of sensory input, coded by unique sparse activation of Kenyon cells [129,130], and to associate them with a simple 'value' - whether this pattern was experienced before in the context of something 'good' or 'bad' [131]. In the case of ant routes, we assume that going back to the nest provides a reward signal that changes output synapse weights on KCs that are activated by the views experienced while moving home. In a realistic simulation of a real ant field site [132], we show the circuit can remember and support recapitulation of routes consisting of 80 or more different views over 8 metres in cluttered environment [133].

Modelling studies [134–136] suggest this route following mechanism could be extended to explain visual homing in ants, bees and wasps, based on the observation that these animals perform learning walks/flights [137–139] enabling them to store numerous views while facing the goal. This would suggest that an innate behavioural routine (learning walks) enables visual homing to be supported by the MB in these central place foragers, while not contradicting a role for the CX in the 'heat maze' visual homing task used for Drosophila [28], where learning walks are not involved. Evidence in ants suggests that they can also resort to other tricks when it comes to home from distant locations [140], perhaps falling back on a mechanism supported by the 'CX'. Computational modelling has also been used to show that the highly processed and compressed visual information provided by the CX ellipsoid body ring neurons [141] is sufficient to solve this task [142].

Models can help bridge the gap that otherwise exists between the identification of brain circuits and the observation of complex behaviours, where direct evidence is extremely difficult to acquire. Moreover, navigation involves an active process of memory acquisition and recall, in which behaviours scaffold the learning process and vice versa. Hence closed loop modelling is particularly useful, and as is the use of ecologically realistic conditions for evaluation. Often the information available is far more noisy or variable than represented in simulations; or the natural situation offers unique cues that the animal can exploit. These considerations are one reason that robotic modelling can be particularly useful [143]. Nevertheless, it is always possible for a model to successfully reproduce the behaviour but turn out to be wrong as an explanation of the mechanism in the animal. In this case, a useful strategy is to examine multiple models while constraining them with as much neural and behavioural information as is available, either neural or behavioural.

Discussion

We have extensive ecological and experimental insight into the capability and mechanisms of navigation in insects, but as outlined above, investigation of the neural circuits lags behind.Perhaps not surprisingly, no circuit purely dedicated to navigation has been found in the insect brain. On the contrary, as we have illustrated above, the data suggest that the same task may be solved in different ways by different individuals or species; and that the same neural processing may be exapted for

different behavioural tasks. Pre-existing circuits will have been exploited in the evolution of new behaviours, such as sophisticated navigational tasks in central place foragers.. Therefore, rather than associating a brain area to a behavioural function, it may be more useful to associate a brain areas with a particular type of computation, and to couple this to understanding the computational requirements of a given behavioural task.

From this viewpoint, the CX and MB seem to offer very different types of computation. The CX integrates a wide range of pre-processed sensory signals, keeps track of the insect's body rotations, and produces outputs which directly modulate locomotion (figure 2). This enables the insect to integrate and display appropriate oriented responses to a vast array of ecologically relevant stimuli. Some behavioural functions such as escape response to predator approach, obstacle avoidance, and attraction to vertical edges in flies and wood ants may be labelled as innate stimulus-responses. Others, such as the ability to deal with passive displacements by computing the compass direction of the impending wind [144], may be branded as remarkable navigational feats even though they require similar computations (figure 2). Synaptic plasticity in the CX could enable the insect to modulate these oriented responses on the basis of experience, i.e., instrumental associations of the reinforcement obtained from directed actions with respect to specific cues [145]. Such a circuit, tracking orientation and incorporating memory, also forms a suitable basis for more complex capabilities such as path integration.

The sparse coding of the MB calyx circuitry, on the other hand, is perfectly suited for the Pavlovian association of numerous arbitrary patterns of activation (whatever their modalities) to a small number of classes given the co-activation of a reinforcer in the lobes [60,131]. This type of computation can serve simple odour-tastant or odour-shock associative learning, but given remarkably little change in the circuitry, can equally be used to learn the panoramic views experienced along a route (Figure 1). The versatility of MB behavioural function is further increased as MB outputs seem remote from descending neurons and could thus feed the learned 'value' of the sensory pattern into pathways contributing to a large variety of behaviours such as extension of proboscis, tracking odour sources, or orientation along a familiar route, among others. Finally, understanding the computational requirements of a behavioural task requires careful investigation of the real sensory motor constraints of the animal, and recognition that different solutions for similar tasks may have evolved, or even developed at the individual level. Consequently, the opportunities offered by new technology for quantifying in detail the movements and information available to a navigating animal is likely to contribute significantly in the future. Constrained by such sensory-motor data on the behavioural side, and a given type of circuitry on the neurobiological side, the space of possible computations can be narrowed down. This offers a promising multi-disciplinary research agenda for the future.

Acknowledgements

Box 1. The importance of naturalistic observations in guiding brain research

Early brain research was strongly inspired by ecology. The seminal paper 'what the frog's eye tells the frog's brain' [146] starts with an accurate description of the frog's behaviour in its natural environment, visual anatomy and physiology. Experimentation (i.e. the display of controlled visual stimuli and recording of neural activity) comes only later in the paper to test whether the optic nerve conveys complex abstractions from the visual image, or so-called 'bug detectors'. If the reductionist approach of experimentation enabled definitive testing for this hypothesis, the constructive approach of naturalistic observations was the key to its discovery.

In insects, many neurobiological studies are grounded in naturalistic observations such as target detection for chasing behaviours [147], escape response to looming cues [148], use of celestial compass [85] or the ability to path integrate [4], among others.

Other studies, however, are derived from human introspection or vertebrate experimental research rather than the insect's natural behaviour, such as abstract visual pattern recognition [149,150], place learning [15,28] ; use of geometry [151] and landmarks [152]. These methods can be valuable for understanding how insect cognitive capacities compare to other species. -. However, in these cases, the task is enforced by the experimenter and care must be taken in assigning function to brain areas. The animal's success in solving the task may reflect that the brain is plastic enough to tap into neural resources ultimately designed to solve another type of task. This is particularly true when using differential conditioning with a generalist reinforcer or painful punisher such as heat or electrical shocks, which could cause synaptic plasticity in widespread regions of the brain.

For instance, Drosophila tethered in a punitive heat visual pattern recognition paradigm learn, for some pair of patterns but not others, to orient its body towards the non-punished pattern [149]. The visual receptive fields of the neurons implicated in solving this pattern recognition task (i.e. central complex R2 cells) [141] filter visual information in a way that is clearly not designed to discriminate such abstract patterns [153]. On the contrary, the stereotypic shapes of these receptive fields [141], suggest that they filter information for specific behavioural purposes; the nature of which requires a better understanding of Drosophila's visual ecology to be clarified. The discordance between experimental task and ecology may explain the baffling failure of flies and bees to discriminate some particular pair of visual pattern in these paradigms. Different pattern

discrimination tasks may thus solicit synaptic modulation in different neural populations [145] that are tuned to different ecologically relevant stimuli.

Similarly, ants' and bees' ability to respond to landmark manipulations in the laboratory led to the implicit assumption that the insect could recognise individual landmarks for guidance. In contrast, naturalistic observations such as the description of spontaneous route following in the field [7,132,154], description of the animal's optics [66,155] and the quantification of the visual information available to the animal in natural scenes [23,53] led to the hypothesis that ants do not need to extract and recognise individual landmarks for navigation but may rather learn the whole panoramic visual pattern projected on their retina, which has been later supported by experimental manipulations [156]. Learning the full view involves drastically different kinds of computation than object/landmark extraction, and consequently points to different brain structures; for example, the MB seems particularly suited to learn large numbers of arbitrary panoramic views perceived during route following [133].

Box 2. Outstanding questions

Circuits: What is the nature of the visual information that the MB receives as input? What connections, if any, can be found between the CX and MB? What other areas of the brain might be significant to navigation, due to multimodal inputs, high level processing function, learning or other relevant characteristics? What is the neural basis of motivational switching in navigation?

Behaviour: Can we pin down the details of the moment-by-moment control of direction in a navigating animal? What are the limits of what a navigating insect can learn? What is the actual accuracy that the brain is capable of supporting, under what external noise constraints?

Computation: How can accurate integration (to support PI) be performed in a neural network? Is it plausible that an insect brain can store multiple eidetic memories? What are the potential mechanisms for dealing with the delayed or indirect rewards typical of navigational learning?

Methodological: Is it possible to devise experiments that allow neural manipulation and measurement but maintain ecological validity? Might certain animals (particularly some not yet well studied) offer methodological advantages to answer specific questions? How can we build and test sufficiently large scale models to encompass the complex, closed loop behaviour that is navigation?

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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 synapse 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 (MBONs), 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 MBON. As a result, the MBON 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 MBONs 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-MBON decrease rather than increase in synaptic strength [157]. As a result, each MBON carries information about a specific value associated to specific odours and can then participate in the elaboration of a variety of behavioural response, such as proboscis extension in honeybees (from [158] or the chemotactic response in Drosophila larvae (from [159]. Additional significant features of the circuit not illustrated here include substantial recurrent connectivity from MBON to KC, and the bifurcation of KC axons into different lobes which may serve different functions.
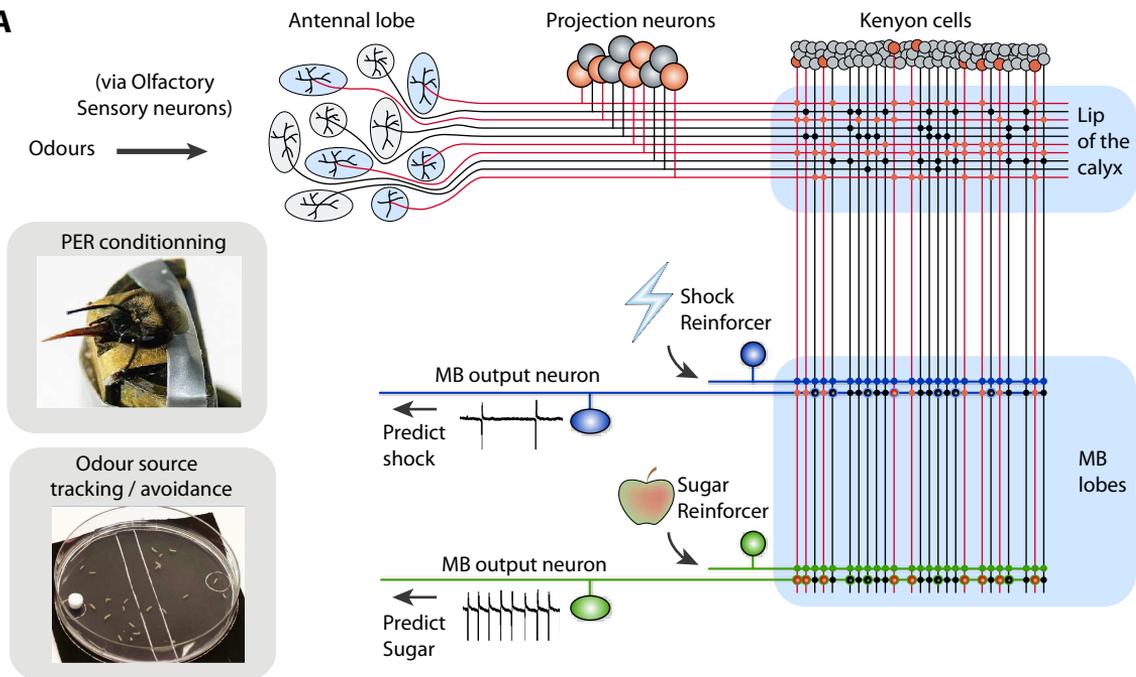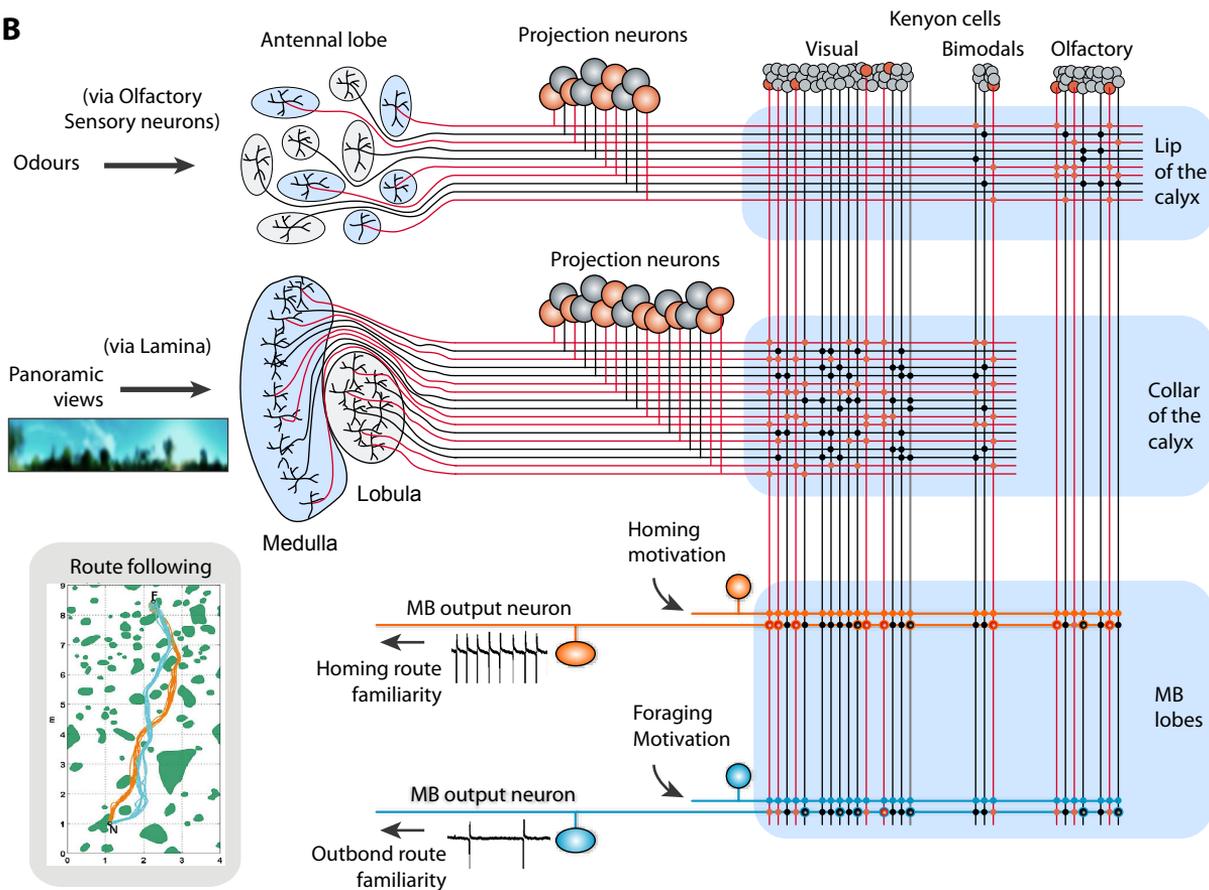
B) The same type of circuitry can equally be used to store pattern of visual information such as the full panoramic views perceived while navigating along a route [133]. This simply requires input from the visual optic lobes, from which PNs are known to synapse into KCs in the collar of the MB calyx in ants and bees. Pattern of activations in these 'visual' KCs would thus be specific to a particular view perceived at one particular location in the world. Some KCs sample only visual information, other only olfactory information and some, at least in ants, integrate both olfactory and visual information [160,161]. All type of KCs could project onto the same MBON, which would thus mediate information about the multi-modal familiarity of the current location. Ants are known to recapitulate their route by moving along these corridors of familiarity involving both learnt views [154] and learnt odours [162]. To maintain route polarity, ants homing and foraging memories are

isolated and accessible only in the appropriate motivational state [163], as seems to be the case with olfactory memories and feeding motivation in adult Drosophila [164].
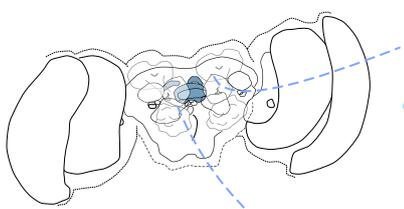
Figure 2. Computation in the Central complex can serve various behavioural tasks.

A) [Schematic modified with permission from [116]]. The central complex (CX) includes several inter-connected neuropils located along the midline of the insect brain (PB: protocerebral bridge; CBU: upper central body; CBL: lower central body (ellipsoid body); No: noduli). Its anatomical organisation shows an ordered neural lattice of 16-18 vertical slices intersected by horizontal layers. The neuropils are precisely connected by repeated sets of inter-hemispheric columnar and tangential cells [115]. Sky compass [85], idiothetic and terrestrial visual inputs enable the representation of spatial azimuthal direction across the 16 slices and, given short term memory of their activation, enable tracking of the animal's rotation [47]. It remains to be seen how odometric information could be combined to keep track of the animal position via path integration. The CX also receives input from pre-processed stimuli such as looming cues [165] or vertical edges detectors [141]. There is surprisingly little connectivity between the CX and the MB, but a small number of neurons [166] may convey learnt information. Such a convergence of behaviourally relevant information makes the CX a likely candidate for their integration into a final locomotor decision. Output in the lateral accessory lobes (LAL) synapse onto descending neurons towards thoracic local control circuit, modulating the insect direction of motion [167]

B,C) It can be hypothesised that the CX keeps track of the direction of behaviourally relevant cues relative to the insect's body orientation, even when they are no longer perceived by the animal sensory system. This type of computation could serves various behavioural functions and explain results observed in different tasks; such as B) the tendency of flies to turn towards an attractive visual bar even when it is no longer present [168] or C) the ability of desert ant to retrieve and orient along the compass direction of the wind after being blown away, even though wind is no longer present [144]. Such capacities could be elaborated by integrative memory into maintainnce of a home vector during long, convoluted excursions.

A

Antennal lobe — Projection neurons — Kenyon cells

(via Olfactory Sensory neurons)

Odours

Lip of the calyx

PER conditionning

Odour source tracking / avoidance

Shock Reinforcer

MB output neuron

Predict shock

Sugar Reinforcer

MB output neuron

Predict Sugar

MB lobes

B

Antennal lobe — Projection neurons — Kenyon cells

Visual — Bimodals — Olfactory

(via Olfactory Sensory neurons)

Odours

Lip of the calyx

Projection neurons

Panoramic views

(via Lamina)

Medulla — Lobula

Collar of the calyx

Route following

Homing motivation

MB output neuron

Homing route familiarity

Foraging Motivation

MB output neuron

Outbond route familiarity

MB lobes

A Insect brain   Central complex

PB
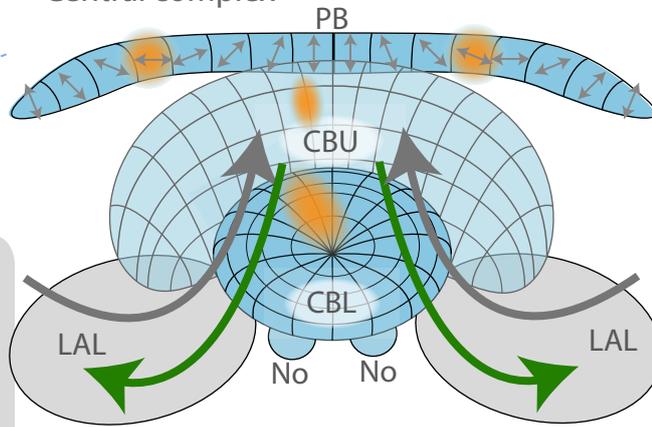
OUTPUT

Directional decision

(modulation in LAL of decending neurons towards local control circuit of legs movements)

CBU

CBL

LAL   No   No   LAL

INPUT

Idiothetic cues

Compass cues
(sky polarisation pattern, celestial bodies, chromatic gradient...)

Egocentrically percieved terrestrial cues:
- pre-processed innate/plastic information (e.g., looming cues, vertical shape detectors, wind, pheromones trail/plume, touch...)

- learnt information from MB ?
(e.g., visual scene familiarity, learnt odour attraction/repulsion...)

COMPUTATION

tracking rotation
- idiothetic cues
- visual cues
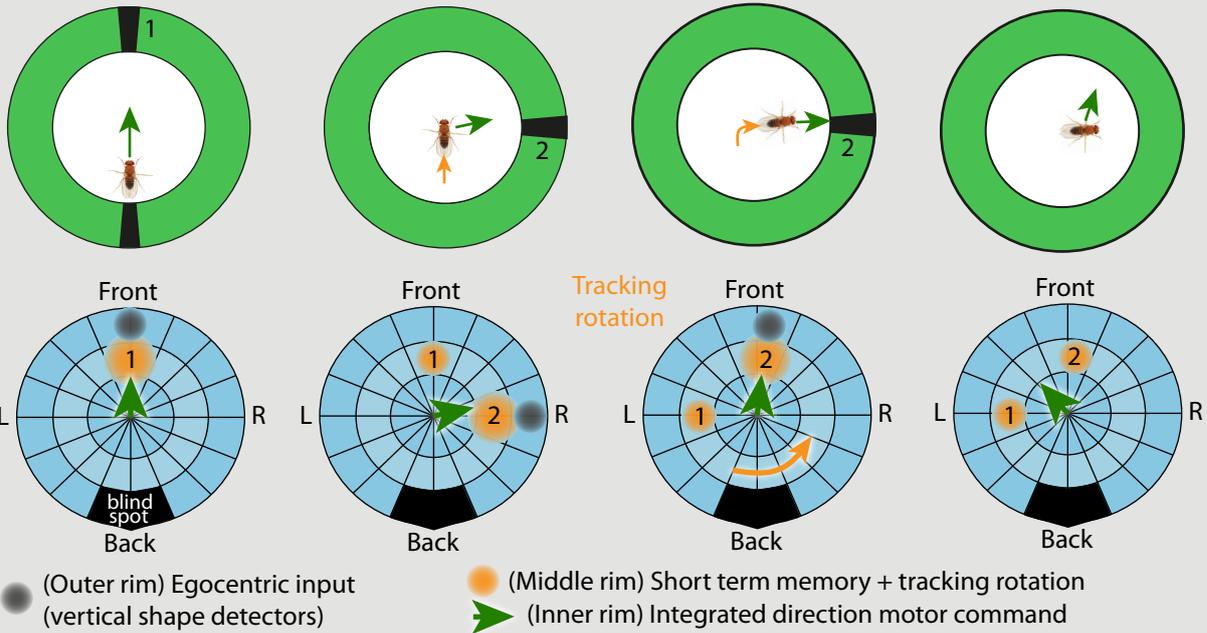- celestial compass cues
- short term memory

tracking position?
- compass cues
- odometric cues ?
- labile memory ?

multiple directional cues integration ?
- path integration
- innate/plastic information
- learnt information ?

B

Tracking rotation

Front   Front   Front   Front

L   R

blind spot

Back   Back   Back   Back

● (Outer rim) Egocentric input (vertical shape detectors)

🟠 (Middle rim) Short term memory + tracking rotation

➤ (Inner rim) Integrated direction motor command

C

Wind gust

Clutching behavioural reflex

Tumbling during passive displacement by wind

Tracking rotation (recovery with celestial compass)

Front   Front   Front

L   R

Back   Back   Back

● (Outer rim) Egocentric input (wind detectors)

🟠 (Middle rim) Short term memory + tracking rotation

➤ (Inner rim) Integrated direction motor command