Multimodal sensory integration in insects—towards insect brain control architectures

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Abstract
Although a variety of basic insect behaviours have inspired successful robot implementations, more complex capabilities in these 'simple' animals are often overlooked. By reviewing the general architecture of their nervous systems, we gain insight into how they are able to integrate behaviours, perform pattern recognition, context-dependent learning, and combine many sensory inputs in tasks such as navigation. We review in particular what is known about two specific 'higher' areas in the insect brain, the mushroom bodies and the central complex, and how they are involved in controlling an insect's behaviour. While much of the functional interpretation of this information is still speculative, it nevertheless suggests some promising new approaches to obtaining adaptive behaviour in robots.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Insects and other arthropods have inspired robotics research for some time. Robots have been built which mimic, for example, fly flight stabilization [1] and obstacle avoidance [2], ant polarization vision [3] and landmark navigation [4], the phonotactic behaviour of crickets [5], or the lobster's ability to locate chemical sources in marine environments [6]. Despite such examples of how insect biology has been of use to robotics (and at times, the robotics of use to insect biology) insect nervous systems have as yet been under-exploited as a potential source for robot control architectures. As we will discuss in this paper, many examples of insect behaviour require the integration of information from multiple sensory modalities, learning, and simultaneous control of several interacting behaviours, enacted by a complex body morphology. These are all problems that are not yet well solved in robotics. The insect brain should offer us some 'proven' solutions to these problems.

Most insect-inspired robot research has been undertaken within single sensory modalities, focused on relatively simple behaviours, or stressed how insect systems suggest simple solutions to various sensorimotor coordination problems. This seems to have created the (false) impression that insects only perform 'reactive' behaviour [7], and that more complex control will need to be modelled on 'higher' animals, for instance: '... intelligence is necessary for organisms which have the burden to manage the complex sensory and motor organs required for complex tasks ... "complex organs" ... would be useless for an insect and, in general, for an organism that could only rely on reflexive processing modules, although adaptable' [8].

Insects are equipped with multiple sensory channels which serve a wide variety of important functions in an insect's behavioural repertoire. These functions include 'identification of events or objects through matching of heterosensory inputs, detection of meaningful stimulus combinations for processes of learning and memory, adjustment of body posture and goal-directed movement by integration of self-generated and external sensory input, and adjustments in sensory attention and triggering of escape responses through convergence of various novel and potentially threatening stimuli' [9]. Path integration, as exhibited in desert ants for example, relies on a variety of sensory signals, including proprioception
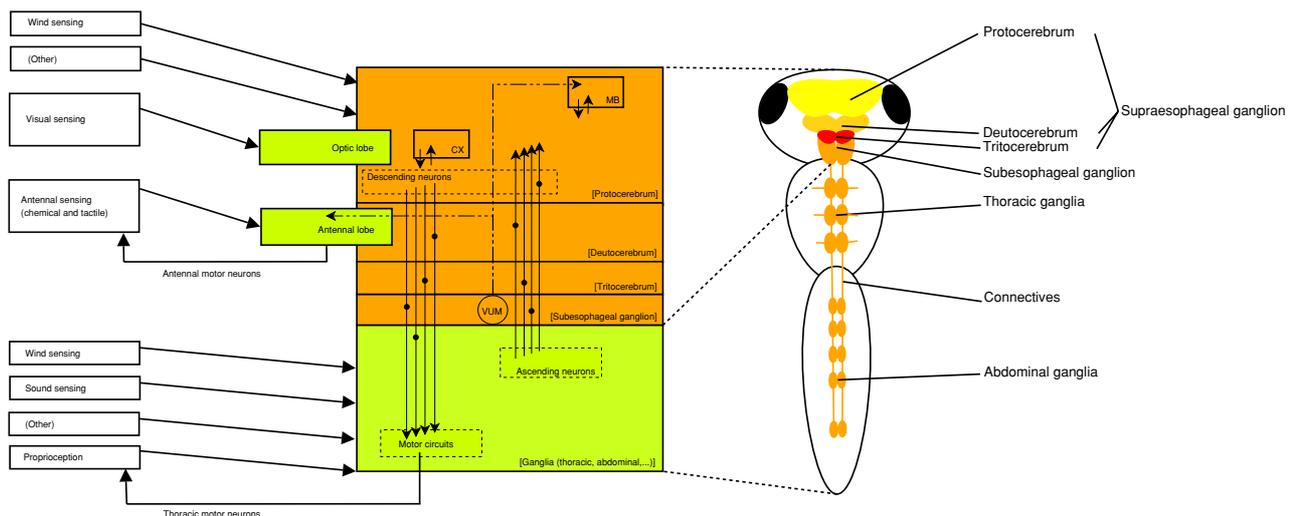
Figure 1. The nervous system of a generalized insect. The brain (supraoesophageal ganglion) consists of proto-, deuto- and tritocerebra and is connected to the suboesophageal ganglion which in turn is connected to the nerve cord linking the thoracic and abdominal ganglia. Schematic diagram showing the main sensory neuropils and the main sensory channels associated with each. The higher brain centres in insects have been reported to be involved in multimodal sensory integration for controlling an insect's behaviour. The mushroom bodies (MB) and the central complex (CX) are located in the protocerebrum. An instance of a value system (VUM), signalling salient sensory events, has been located in the suboesophageal ganglion. Refer to text for further explanations.

('step counting' [10]), vision (optic flow, polarized light), and the memory and update of a homing vector. Some insects are capable of spatial navigation by landmarks over several kilometres, storing and remembering spatial information about landmarks, possibly as photograph-like, 'snapshot' (eidetic) images (e.g. [11]), or as a set of parameters or features extracted during learning flights [12]. Experimental studies on pattern perception in bees show that these animals can categorize visual stimuli based on the features the stimuli are composed of [13]. Analogues of attention have recently been investigated in the fruit fly [14–16]. Morasso *et al* [8] mention 'manipulation' as a significant 'higher capability' needing more complex control in vertebrates, but many tasks achieved by insects require the manipulation of objects (e.g., [17]). Elementary forms of cognition (such as operant conditioning for visual pattern avoidance [18, 19]), and context generalization (e.g., extracting the sensory signals predicting salient events and separating these from non-predictive signals [20]), and impressive navigational skills (e.g., [21–23]) suggest insects have rather more to offer robotics than merely reactive behaviours.

Insects have rich and interesting behavioural repertoires, yet have a central nervous system and genome of a size that can (at least in principle) be studied thoroughly and systematically. Complex control of *perception for action* may therefore be understood in these systems before they can be understood in vertebrates. In an attempt to discover useful design principles for an insect-inspired control architecture, this paper considers a range of biological and neurobiological evidence (following Weiner's guideline that 'generality must be discovered, it cannot simply be declared' [24]). The aim is to provide an overview of current evidence regarding multimodal sensory integration in the insect brain, the organization of behaviour, and what kind of control architecture this suggests. We will first describe general features, then focus the discussion on two highly structured brain areas involved in multimodal sensory integration, the mushroom bodies and the central complex, before sketching a functional specification of an 'insect brain' architecture.

2. General features of the insect central nervous system

2.1. Basic anatomy

An insect's external anatomy can be divided into the head, the thorax, the abdomen and appendages. Like many arthropods, insects have a nervous system consisting of a series of ganglia (large aggregates of neurons) linked by connectives (thick bundles of axons). These form the brain in the head and a nerve cord extending through the thorax to the abdomen; see figure 1.

The insect brain consists of two head ganglia: the supraoesophageal and the suboesophageal ganglia. The supraoesophageal ganglion, which in size ranges from about 10^5 neurons in the fruitfly to 10^6 in the honey bee, consists of three major parts: the proto-, the deuto- and the tritocerebrum. The protocerebrum includes the optic lobes receiving input from the compound eyes and the ocelli (simple single lens eyes only sensitive to light intensity). The protocerebrum also hosts 'higher' brain centres, such as the the mushroom bodies and the central complex, which are sites of multisensory convergence that will be discussed in detail below. The deutocerebrum processes information collected by the insect's antennae, consisting of two distinct areas, the antennal lobe and the antennal mechanosensory and motor centre [25]. The tritocerebrum and suboesophageal ganglion are linked to taste perception and sensing and motor control of the mouthparts (e.g. [26]).

The suboesophageal ganglion physically links the supraoesophageal ganglion with the ventral nerve cord. Signals from the brain pass to the nerve cord via a few hundred 'descending' axons. In the thorax, pairs of thoracic ganglia (typically containing a few thousand neurons each) control wing and leg movements, but also receive sensory inputs from these appendages (proprioception, mechanoreception—in crickets, sound) and may relay these to the brain via 'ascending' axons. Abdominal ganglia receive input from a large number of sensory receptors located at the insect's rear, such as cerci hair-cells, genitalia, etc. Note that each ganglion of the ventral nerve cord (including the deutocerebrum, tritocerebrum and suboesophageal ganglion in the head) receives sensory input and at the same time controls some respective body parts (e.g., antennae, mouthparts, legs, wings, gut, genitalia or stinger). Figure 1 illustrates the nervous system of a generalized insect.

2.2. Decentralized control

Insect nervous systems exhibit decentralization: many overt behaviours (e.g., feeding, locomotion, mating) are, to varying extents, controlled by body ganglia instead of the brain. For example, much of the processing for individual leg control and coordination is delegated to the thoracic ganglia of the ventral nerve cord [27] where it is controlled by a range of proprioceptors (e.g., receptors providing information about joint angles, muscle contractions and load) and exteroceptors (e.g., hairs on an insect's foot that excite sensory neurons when the foot is placed on the ground) connected directly to their leg-specific thoracic ganglia. The thoracic ganglia also control swing patterns and spatial placement of legs. A review of information flow in leg control is presented in [28]. Descending axons from the brain or suboesophageal ganglion modulate thoracic circuitry [29, 30], for example, to initiate, suppress and maintain walking behaviour, or determine speed and direction of locomotory behaviour. Note this general organization is similar to that found in vertebrates, where circuits in the spinal cord are responsible for producing rhythmic motor patterns and basic reflex responses, but are modulated by descending signals from the brain-stem and cortex.

2.3. Specialized pathways

Insect behaviour is often viewed as a collection of parallel, highly specialized *domain-specific* sensorimotor loops, each of which reflects a particular solution to an ecologically relevant problem. For the case of the honeybee, such modules may include circuitry for (i) 'pheromone-released behaviours: aggression and defence, (ii) distance estimation from the visual flow field experienced during flight, (iii) path integration during search flights,...' [31]. Such loops may or may not pass through the brain. Escape responses triggered by hair-cell detection of wind flow involve direct connections from abdominal to thoracic ganglia [32]; whereas auditory localization involves ascending and descending pathways between the thoracic ganglia and the brain [33]; and antennal-triggered escape involves sensory input directly to the brain

[34]. Reflexive behaviour in insects involves filtering for relevant sensory cues, which may be determined by the morphology of receptors as much as more central processing. Wehner [35] described sensory systems as *matched filters* to illustrate how animals solve problems, apparently requiring sophisticated information processing solutions, by exploiting sensory mechanisms uniquely matched to the behavioural tasks. For example, in visually-guided behaviours in flies, the optomotor response depends upon the average relative rotation of the visual field [36] whereas for the landing response speed control is achieved by keeping the optic flow velocity constant, thus assuring that flight speed is approaching zero at touchdown [37].

Although some loops, such as those just mentioned, involve single sensory channels, others integrate sensory information from multiple sensory modalities, e.g. descending neurons reporting course deviations in the locust *Locusta migratoria* show ocellar, visual and mechanosensory responses [38, 39]. Similarly, gaze stabilization in the blowfly *Calliphora* is controlled by a variety of distinct sensory processes [40]: compound eyes, ocelli, halteres, wing-load sensilla, gravity and head posture all contribute. These pathways carry out fast transformation of sensory signals into appropriate motor commands. Such examples illustrate the specialization of perceptual systems, dividing intelligent solutions to ecologically relevant problems into domain-specific modules. However, this is not the whole story for insect behavioural control.

2.4. Behaviour coordination and learning

Reflex-loops form the basis of the 'insect brain' architecture. Simple interaction of different reflexes could be through addition (summing the effects of various reflexes) or switching (inhibition of one reflex by another), with different reflexes having different gains or priorities. Thus far it resembles Brooks' subsumption architecture [41], with behaviour partitioned into a set of task-oriented activities, each with their own sensing and control requirements, and a partial ordering among them to build more complex systems. However, insect systems show a substantially greater variety of modes of interaction: this can occur at the level of sensors, sensory neurons, sensory interneurons, or ascending neurons; or in the brain, descending neurons, motor interneurons, motor neurons or even the muscles [42].

More importantly, collections of interacting reflex-loops are insufficient for explaining the behavioural complexity of insects, such as the examples discussed in the introduction. According to Menzel and Giurfa [31], the problem of organizing parallel domain-specific sensorimotor pathways requires *central integration* where information from domain-specific modules is combined to form new behaviours and new solutions to ecologically relevant problems. Okada *et al* [43] similarly propose that parallel, domain-specific, processing streams are subject to experience-dependant modification by association areas in a hierarchical fashion. Okada *et al* label the mushroom bodies and the central complex as 'association areas'. Neurobiological evidence suggests that

these areas play particularly important roles in multimodal sensory integration, modulation of reflexive, sensorimotor pathways and learning. Hence we will next provide an overview of these areas.

3. Higher brain centres

The insect's protocerebrum contains many complex and little understood neuropils (anatomically distinct dense networks of axons and dendrites). Two architecturally distinctive neuropils, the mushroom bodies and the central complex, have been widely investigated for their apparent role in controlling more complex behaviours. The next sections will review their anatomy and neuroarchitecture, and their possible behavioural functions.

3.1. The mushroom bodies (Corpora pedunculata)

3.1.1. Anatomy and connectivity. The mushroom bodies are a pair of large and distinctively (mushroom-)shaped neuropils in the insect brain. In honeybees, they together contain around 340 000 neurons (the bee brain contains approximately 960 000 neurons occupying 1 mm^3 [31]). Though smaller in many other insects, they still comprise a significant proportion of the total brain neurons. The mushroom bodies in most insects have a similar and characteristic neuroarchitecture: namely, a tightly-packed, parallel organization of thousands of neurons, called Kenyon cells. The mushroom bodies are further subdivided into several distinct regions: the calyces, the pendunculus and the lobes. The dendrites (inputs) of the Kenyon cells have extensive branches in the calyces[1], and the axons (outputs) of the Kenyon cells run through the pendunculus before bifurcating, diverging and extending to form the typical α- and β-lobes[2]. Synaptic interconnections between Kenyon cell axons have been reported [46]. The structure is thus summarized by [47]:

- 'the input and the output of activity due to extrinsic fibres [i.e. neurons with cell bodies external to the mushroom bodies] takes place in separate neuropil areas (calyces and lobes)';
- 'the *Corpora pedunculata* represent a multi-channel system of intrinsic fibres [i.e. neurons with cell bodies internal to the mushroom bodies] with respect to the afferent (input) and efferent (output) pathways of extrinsic fibres'.

Note also that there is considerable divergence (1:50) from a small number of extrinsic input neurons onto the large number of Kenyon cells, and considerable convergence (100:1) from the Kenyon cells onto extrinsic output neurons[3].

In most insect species, the mushroom bodies receive significant olfactory input. Interneurons relay odourant information from the olfactory receptors, via the antennal lobe in the deutocerebrum, to the mushroom body calyces. In the

cockroach and locust, tactile and gustatory input have also been reported. Some Hymenoptera, e.g. bees and wasps, have substantial connections from the optic lobes on both sides of the brain to the calyces of both mushroom bodies [49]. The absence of direct visual input in other species does not necessarily mean that visual information is not integrated. Rather, it may be preprocessed in other areas of the protocerebrum before feeding into the mushroom bodies [20]. Neurons in the calyx of the cockroach have been reported to respond to antennal movement; these signals may be proprioceptive in origin [50]. There is also evidence of possible input from circadian clock neurons in *Drosophila* [51].

Sensory afferents exhibit ordered connections with the calyces of the mushroom bodies. For example, terminals of input neurons onto the calyces of the cockroach and of the honeybee exhibit function-specific distribution patterns [52] and the calyces show a modality-specific topography [9]. At least some of this ordering is preserved by the Kenyon cells. Mushroom bodies in honeybees are subdivided into several sensory compartments [53] and modular structures in the mushroom bodies of the cockroach are reported in [54]. A recent *Drosophila* study has shown that Kenyon cells are subdivided regularly regarding their gene expression, suggesting extensive parallel compartmentalization of function [55].

The activities of extrinsic neurons in the output regions of the mushroom bodies can be classified as (i) sensory, (ii) movement-related and (iii) sensorimotor [56]. A large majority exhibit responses to multiple sensory stimuli and therefore confirm the suggestion that the mushroom bodies participate in sensory integration. For example, in the cricket a single neuron was reported to respond to auditory, visual and wind stimuli [57]. These neurons also exhibit changes in activity and sensitivity levels which can be related to specific stimuli and stimuli combinations. Electrical recordings of single neuron and field potential activities also indicate that processing of sensory stimuli can last from seconds to sometimes minutes after stimulation [46]. This is likely to involve recurrent feedback: it has been shown that extrinsic neurons provide direct recurrent feedback to the calyces [58] and indirect feedback via other areas [53]. However, despite some examples of motor-related activity in extrinsic output neurons (see below), there is little evidence of direct connections to descending neurons. The majority of output pathways target a variety of other protocerebral regions [59–61]. A good account of the output connections of the mushroom bodies to other parts of the brain can be found in [44].

3.1.2. The mushroom bodies are secondary pathways. Evidence suggests that mushroom bodies do not form the only sensorimotor pathway for any modality. Most sensory areas in the brain have direct connections to premotor areas, and thus to descending neurons. The same sensory areas also supply afferents to the mushroom bodies (either directly or indirectly) as part of a secondary pathway as shown in figure 2 [50]. For example, in most insects, the olfactory

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[1] The calyces may be a later evolutionary addition of a specific input structure to a more primitive mushroom body architecture [44].
[2] There are exceptions to this description of the typical Kenyon cell e.g., not all Kenyon cells bifurcate [45].
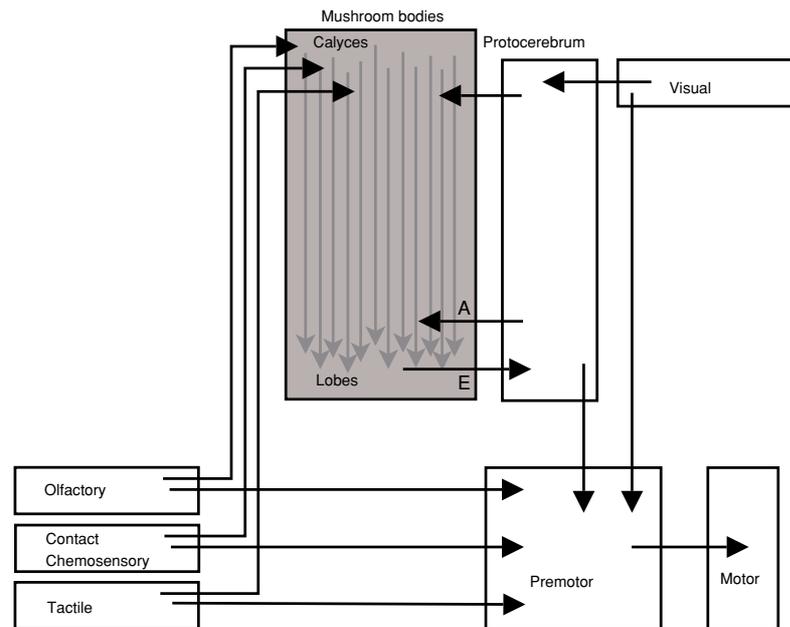[3] These ratios are estimates based on data from [48].

Figure 2. Evidence suggests that mushroom bodies do not form the only sensorimotor pathway for any modality. Sensory areas in the brain have direct connections to premotor areas, and thus to descending neurons in motor areas. The same sensory areas also supply afferents to the mushroom bodies (either directly or indirectly) as part of a secondary pathway. This schematic overview of the connections is drawn after [50].

system consists of two parallel pathways as depicted in figure 3. The main olfactory pathway is the connection between the antennal lobe and the superior lateral protocerebrum (medial and outer cerebral tract). The mushroom bodies are part of a secondary pathway (inner cerebral tract). Convergence in the superior lateral protocerebrum of antennal lobe outputs and mushroom body outputs provides a locus for comparison of information processed in these neuropils [61]. Similarly to the olfactory pathway, a secondary pathway via the mushroom bodies has been reported for the conditioning of the proboscis extension reflex in the bee [62]. A direct connection from the antennal lobe to the motor neurons of the mouthparts has a secondary parallel pathway branching off via the mushroom bodies. Genetic and developmental impairment of mushroom bodies confirm the hypothesis of parallel secondary pathways. Impaired *Drosophila* can perceive but cannot remember odours, and their overall behaviour was described as 'normal' [46].

3.1.3. Functional roles of the mushroom bodies. The size, distinctive architecture, range of inputs and outputs, and parallel pathway arrangement raise obvious questions about the functional role of the mushroom bodies in insect behaviour. We will here discuss the main current hypotheses.

A role in pattern recognition. The parallel channels of intrinsic Kenyon cells perform specific processing functions on the mushroom body input. Heisenberg [63] speculated that the large divergence of sensory afferents onto the calyces of the mushroom bodies may form matrices where each element (Kenyon cell) could be specific for unique relationships of excitations in the primary sensory channels feeding the

mushroom bodies, indicating a particular stimulus situation. The dendrites of extrinsic (output) neurons, invading the lobes, vary in size and arborization patterns. Thus each imposes different characteristic filter parameters on signal transmission from the Kenyon cells, depending on how many and which of the Kenyon cells it interacts with [49]. In support of this idea, some extrinsic output neurons have been shown to respond with changes in sensitivity and activity levels to a certain modality only when also presented with another [57]. The topographical relationships between efferent dendrites extending across Kenyon cell axons and how these axons represent afferent projections in the calyces is discussed in [64].

Kenyon cells may also act as delay lines [47, 53] which could provide a mechanism for recognizing temporal patterns in the input. Schuermann suggests 'the peculiar form of the Corpora pedunculata due to the pedunculi and lobes is . . . a special arrangement of neurons for transposition of synaptic distances into sequential activation or inhibition of nerve fibres'. Some extrinsic neurons have been reported to increase or decrease their activity depending on some preceding stimulus [57].

Note that pattern recognition also has a role in learning as further discussed below—sparse coding of sensory inputs is said to 'make neurons more selective to specific patterns of input, hence making it possible for higher areas to learn structure in the data' [65]. More generally, Ito *et al* [59] caution that the learning and memory deficiencies observed after disrupting or ablating the mushroom bodies could indicate that their critical role is in preprocessing of signals (such as detecting complex spatiotemporal patterns) for subsequent learning, rather than that they are themselves the central site in which learning and memory take place.
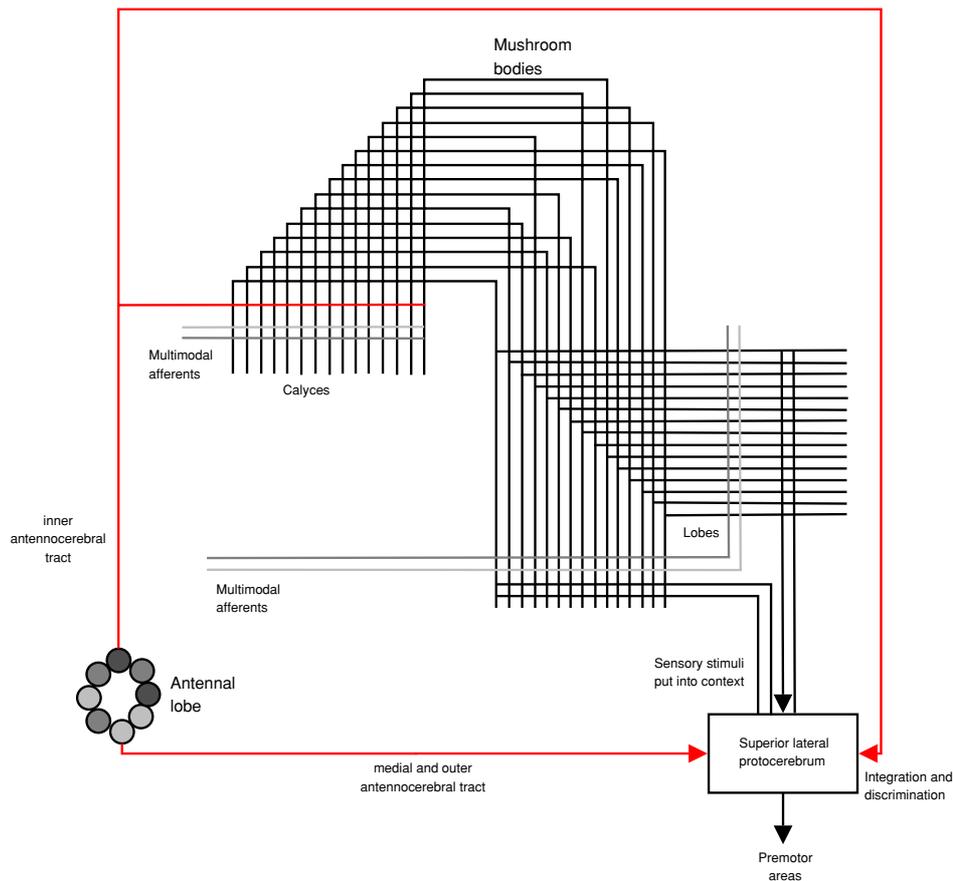
Figure 3. Hypothesized integration stages of odour perception with other sensory modalities (redrawn from [61]). Odours are represented by spatio-temporal patterns in the glomeruli of the antennal lobe. The inner antennocerebral tract projects to the calyces and continues into the superior lateral protocerebrum whereas the medial and outer antennocerebral tracts project directly into the superior lateral protocerebrum. In the mushroom bodies, odours are placed into a multimodal context and efferents relay this information into the superior lateral protocerebrum. There, antennal lobe and mushroom body outputs converge and it is speculated that the relevance of odours is assessed with respect to the multimodal context, integrated and discriminated before feeding into premotor areas.

A specific example of how the mushroom bodies perform sophisticated recognition is given by studies of the olfactory pathway in locusts [66–68]. Different odours produce distinctive spatio-temporal patterns in the antennal lobe. Laurent and Perez-Orive hypothesise the Kenyon cells help disentangle the spatio-temporal codes by operating as coincidence detectors selective for correlations in the input spike trains. Kenyon cells receive direct excitatory input from antennal lobe projection neurons, but also indirect inhibitory inputs from the same neurons via lateral horn interneurons, arriving shortly after the excitation. Thus the integration time for the Kenyon cells is limited to short time windows [69], making them highly sensitive to precise temporal correlations. The suggestion is that while antennal lobe processing supports basic olfactory learning, more subtle odour discrimination tasks require the mushroom bodies [70]. Evidence from bees supports this interpretation. Bees with disrupted mushroom bodies were capable of distinguishing dissimilar odourants, but could not distinguish similar ones [71].

A role in integrating sensory and motor signals. Although most discussion of 'integration' in the mushroom bodies focuses on the combination of sensory inputs, it should be recalled that they also receive recurrent feedback, and that extrinsic neurons show motor-related responses. In the cockroach *Periplaneta americana*, some mushroom body extrinsic neurons are reported to exhibit activities for 100–2000 ms preceding the onset of locomotion [43]. This is much earlier than activity seen in descending neurons which usually precedes movement by only 10–200 ms. The timing also precludes the response being due to feedback from proprioceptive sensors during movement. Okada *et al* [56] report extrinsic neuron responses which are selective to the directions of turning behaviours. These researchers propose that the mushroom bodies participate in the integration of sensory stimuli and motor signals, possibly playing a role in initiating and maintaining motor action, or patterning motor output [72]. Supporting evidence is that the mushroom bodies play an important role in the termination of active walking phases in *Drosophila* [73]. However, ablations of the mushroom bodies did not prevent spontaneous locomotory behaviour; hence, it is thought that an indirect pathway involving the mushroom bodies converges with more direct pathways for hierarchical integration and modulation of

behaviour, perhaps including the central complex, discussed below.

Furthermore, extrinsic mushroom body neurons of cockroaches have been reported to discriminate self-administered antennal grooming from externally imposed antennal stimulation [72]. A fascinating possibility is that the mushroom bodies are more generally involved in integrating efferent copies with reafferent signals, thus enabling insects to learn to discriminate self-stimulation from environmental stimulation [74].

Neural substrates for learning. It is widely acknowledged that the mushroom bodies play some important role in associative learning and memory, with evidence from a variety of insect species, insect behaviours and experimental manipulation methods. For example, mushroom body ablation has been reported to impair short-term and long-term memory of courtship conditioning in *Drosophila* [75]; genetic mutants with structural α-lobe defects have shown deficiencies in long-term memory [76]. The mushroom bodies of the cockroach *Periplaneta americana* have been linked to visual place memory [50]. There is a positive correlation between the volume of the mushroom bodies and sophistication of social behaviour in Hymenoptera (cf, [77]), and mushroom body volume increases are linked to behavioural development [78], e.g., learning the location of the hive when commencing foraging [79]. However olfactory learning has been the main focus of investigations to date.

Kenyon cells show striking structural plasticity, shedding their fibres and growing new ones at various occasions in an insect's lifetime [63]. In [80], evidence suggesting the mushroom bodies in *Drosophila* are the site of a memory trace is reviewed and evaluated. Gerber *et al* [80] elaborate on criteria for a memory trace (presence of neural plasticity in the mushroom bodies, the sufficiency and necessity of this plasticity for memory, and whether memory is abolished when input or output to the mushroom bodies is blocked during testing) and conclude that localizing the olfactory associative memory trace to the Kenyon cells of the mushroom bodies is a reasonable working hypothesis. Indeed, the Kenyon cells of the *Drosophila* mushroom bodies have been identified as a major site of expression for a number of 'learning' genes (for a review, see [81]). According to Dubnau *et al* [81], Hebbian processes underlying olfactory associative learning may reside in Kenyon cell dendrites. However, synaptic plasticity underlying olfactory memory has also been located in the synapses connecting Kenyon cells to extrinsic neurons [82].

Based on the mushroom bodies' functional anatomy, particular odours are assumed to be represented by specific subsets of Kenyon cells. For any odourant to become a predictor of a given reinforcing event (e.g. sucrose reward), the output synapses of particular sets of Kenyon cells should be modified such that extrinsic mushroom body neurons could then mediate a conditioned response (e.g. approach or avoidance). In [83], the response of one particular extrinsic mushroom body neuron *Pe*1 was studied extensively in the context of non-associative and associative learning. It was shown to change response in various conditioning paradigms,

and hypothesized to be an element for short-term acquisition of an associative olfactory memory in the honeybee. In the honeybee, the role of appetitive reinforcement has been shown to have a neural substrate, an identified neuron called VUM$_{mx1}$ located in the suboesophageal ganglion [31, 62, 84, 85] which arborises into the antennal lobe, the mushroom bodies and the lateral horn. Stimulation of this neuron has the same effect as presentation of a sucrose reward for classical conditioning of the proboscis extension reflex [62, 84]. In the fruitfly, the paired dorsal medial (DPM) neurons arborise throughout the mushroom body lobes. In genetic studies these neurons have been shown to play a modulatory role (said to provide negative reinforcement) in olfactory learning and memory formation [86, 87].

3.2. The central complex

While the exact function of the mushroom body is not certain, it is clear that it has major roles in spatio-temporal sensory processing and learning. By contrast, the role of the central complex remains rather more elusive, but seems to be largely concerned with (pre-)motor processing, control of locomotion, and possibly path integration.

3.2.1. Anatomy and connections. The central complex has a midline-spanning position in the insect brain and a highly regular neuroarchitecture. The common structure of the central complex among arthropod species is reviewed and discussed in [88]. It is situated between the two brain hemispheres and consists of a group of four distinct but interconnected neuropils: the protocerebral bridge, the upper division of the central body (in *Drosophila* also termed the fan-shaped body), the lower division of the central body (in *Drosophila* also termed the ellipsoid body) and the noduli. These neuropils are connected via columnar interneurons. The neuroarchitecture is defined by 16 columns with 8 in each brain half, and a characteristic connection pattern between the two brain hemispheres, as shown in figure 4, which has been found in all species studied so far [9].

The central complex is connected to many other protocerebral regions (but only very few connections to the mushroom bodies have been reported cf, [59, 89]). The protocerebral bridge is considered the main input region [90] with connections from visual regions particularly dominant in locusts and honeybees. Recent research identified memory traces for visual features in the central body of *Drosophila* [91]. Innervations by ocellar interneurons have been reported in a number of insect species (cf, [92]) and also from the polarization vision pathway [9]. Although significant visual input has been shown in a number of insect species, blind insects also have pronounced central bodies which suggests that vision is not the only sensory modality processed by the central complex. Evidence suggests that mechanosensory input is provided to the ellipsoid body from the ventral nerve cord via the lateral accessory lobes in the locust *Schistocerca gregaria* [93].

Detailed anatomical studies of the central complex suggest the anatomy of the central body is well suited to
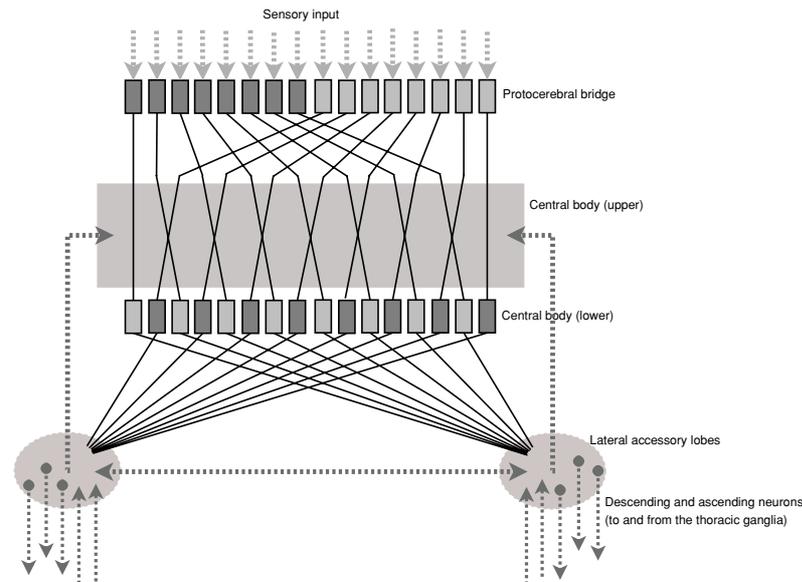
Figure 4. Schematic diagram showing the neuroarchitecture of the central complex (redrawn after [103]). The anatomy of the central complex with regular columnar overlay between sides is well-suited to coordinate inputs from both brain halves.

overlay inputs (received via the protocerebral bridge) from both brain hemispheres [88, 90]. Insects that perform sophisticated asymmetric leg movements (e.g., weaving, comb-building) appear to have a large or elaborate central complex [94]. The lateral accessory lobes, as shown in figure 4, are major output targets of the central complex and interact with the central nerve cord through ascending and descending neurons; there is also feedback from the lateral accessory lobes to the central body (or fan-shaped body) [93]. Neurons from both lateral accessory lobes were also reported to be reciprocally connected in the silk moth *Bombyx mori* [95].

3.2.2. Functional roles of the central complex. Almost two decades ago, it was proposed that the central complex with its precise left-right fibre geometry functions as a well-balanced system of inhibitory and excitatory interactions between the two brain halves [92]. Behavioural and genetic studies of *Drosophila* have associated the central complex with functions related to higher locomotor control; including initiation and modulation of behaviour, and controlling the persistence of behaviours. An excellent review can be found in [96]. It has been proposed that the neurophysiological mechanisms responsible for generating and controlling such highly organized locomotor activity imply a 'higher decision centre' organizing behavioural activity [97].

Producing behavioural activity patterns. Neural activity in the central complex has been linked to the expression of behaviour. Some neurons in the central complex of *Drosophila* have been reported to represent thoracic motor patterns [98]. Activity changes in the connections between the lateral accessory lobes and the central body were linked to initiation and termination of flight in *Schistocerca gregaria* [93]. Distinct activity patterns (measured by staining methods)

for different behavioural situations were reported in [99], not only for flight and walking, but also for different visual stimuli. Bausenwein *et al* reported that activity labelling did not reflect the intensity of sensory stimulation but that it reflected distinct activity patterns for different (visually controlled) behavioural situations, and suggest these can therefore be thought of as central representations of behavioural activity.

Locomotor coordination and regulation. Central complex mutants exhibit a range of locomotion defects. Mutant fruitflies with a disrupted protocerebral bridge were unable to fly and showed abnormal walking and turning behaviours. The protocerebral bridge, and connections from the protocerebral bridge to other regions of the central complex, were reported necessary for maintaining but not for initiating locomotor activity [89]. The protocerebral bridge is involved in regulating and optimizing walking speed by controlling step length [96]. In *Drosophila*, the central complex has generally been found to up-regulate walking activity whereas the mushroom bodies have been shown to down-regulate or suppress locomotor behaviour [73].

Orientation. The overlay of signals in this mirror-symmetrical neuropil has been shown to play an important role in goal-directed motion. Mutant flies, with partially interrupted fan-shaped and ellipsoid bodies along the midline of the brain, were unable to compensate for existing body side asymmetries whereas flies with an intact central complex could deal with such asymmetries [96]. These mutant flies were unable to approach targets in a straight line. Furthermore, flies with intact central complex continue to move towards a target despite the target becoming temporarily invisible and/or a second target distracting the flies [100]. However, some central complex mutations (ellipsoid body and/or fan-shaped body) cause flies to quickly loose their bearings. The inability of mutants to maintain a bearing towards a target also suggests

a role of the central complex for resolving conflicts between sensorimotor pathways competing for behavioural expression.

A centre for path integration. The central complex has recently been pronounced a promising candidate as a centre for path integration. Vitzthum *et al* [101] have identified neurons in the central complex of the locust *Schistocerca gregaria* sensitive to polarized light—polarized skylight patterns are an important stimulus providing compass information [102] for many insects. Additional visual inputs to the central complex, given its apparent importance in controlling locomotory behaviour (e.g., estimating distance or rotation from optical flow), strengthen the argument for the role of the central complex in path integration [103]. Some inputs to the protocerebral bridge are said to originate from the accessory medulla, the circadian pacemakers in the brains of cockroaches and flies [51, 104]. Orientation using celestial cues requires adjustment for their positional changes over the day; thus these circadian inputs may serve time compensation [9]. Note that such a role for path integration is indeed quite consistent with the idea that the central complex is a higher locomotion control centre.

4. Towards 'insect brain' control architectures

Based on the preceding information about insect nervous systems, we here propose a general 'insect brain' control architecture for obtaining adaptive behaviour in robots. Our basic motivation for making this proposal is that insects *work*—they have a range of competences that far exceeds current robot capabilities. It seems sensible to take a close look at insect designs when devising solutions to problems in robotics. This is not a new suggestion, but to date the focus has been on specific sensorimotor systems, rather than the overall organization, or integration of behaviours. This has led to the largely mistaken view that insect control mechanisms can be simply described (sometimes simply dismissed) as a collection of reactive behaviours; and that we must look to mammalian nervous systems, or other engineering approaches such as hybrid control, if we want to 'scale up' to complex robot behaviour.

Like many mistaken views, it has an element of truth, in that perceptual systems of insects did not evolve to build an internal model of the environment for general action, but rather evolved for particular tasks relevant to the animal and its particular ecological niche. Thus, as discussed in section 2.3, there *are* many parallel domain-specific sensorimotor pathways. These pathways form the basis of our proposed architecture, and there are already a number of successfully implemented robot systems based on such pathways that we can draw upon. Behavioural decomposition, and distributed control are features of the nervous systems of insects (and also that of vertebrates, cf, [105]) that resemble the behaviour-based approach to robot control. Behaviour-based systems (in particular Brooks' subsumption architecture) aim at achieving higher levels of competence by adding behavioural modules incrementally. It has been noted that these architectures often fail to scale well as layers are added. In fact, looking at the insect brain, rather than finding ever more
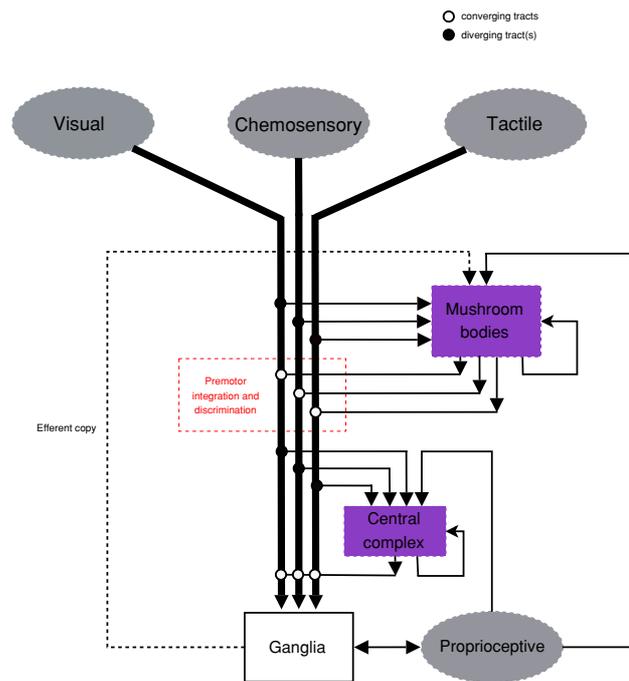

Figure 5. An outline of the proposed model is drawn schematically. Reflexive (domain-specific) sensorimotor pathways form the basis of this architecture. For illustration purposes, three direct pathways are shown for different modalities. Sensorimotor pathways for other modalities could be added (or, for a robot architecture, substituted). Indirect secondary pathways (mushroom bodies) achieve context generalization, associative learning, and modulate reflexive sensorimotor pathways. Additional central coordination (central complex) for integration and persistence of behaviours is necessary and may also be used for path integration. Recurrent connections may serve short-term memory (in both mushroom bodies and the central complex). Efferent copies and forward models will be used to modulate sensory processing according to expected reafference.

layers of 'behavioural modules', there appear instead to be two qualitatively different 'association areas' (the mushroom bodies and the central complex) that act to modulate the direct sensorimotor loops in several important ways.

We thus propose that the next element of our architecture will be an indirect secondary pathway, which forms a parallel route for sensory inflow. This can be used to place information from various sensory modalities into context, to improve on reflexive behaviours by learning to adapt and anticipate reflex-causing stimuli, or learning to substitute one stimulus for another in guiding action. There is good evidence that the mushroom bodies play such a modulatory role in the insect brain and thus their neural architecture provides a model for designing an associative memory capable of multimodal sensory integration and modulating underlying reflexes in a heterarchical, context-dependant manner.

Mathematical descriptions of the ionic currents and the resulting computational properties of Kenyon cells (the intrinsic mushroom body neurons) of the honeybee have already been developed [106, 107]. The mapping of sensory neurons onto Kenyon cells shows high divergence suggesting a form of sparse coding, quite possibly serving the recognition of

unique relationships in primary sensory channels or domain-specific sensorimotor loops (as discussed in section 3.1.3). Recently, system models of the mushroom bodies for odour classification based on this characteristic neuroarchitecture have been proposed [108, 109]. However, this is not simply a feedforward system but involves multiple recurrent connections that are likely to be essential to its function, perhaps providing a mechanism for short-term memory (and resonating sensory events). Associative memory and learning also benefits from value systems, which in insects appear to be implemented in a small number of neurons with many connections throughout the brain. These signal salient sensory events (such as appetitive reward) and are involved in the plasticity of the mushroom bodies. These value systems report activity in reflex-loops, helping to establish useful CS-US relationships.

The third element of our proposed architecture is inspired by the central complex, which forms another parallel processing stream superimposed on more direct sensorimotor loops. The central complex has a remarkable neuroarchitecture and many functions of the central complex in coordinating locomotory behaviour are well described. Central integration of sensory and motor signals is needed to coordinate behaviours, overlay signals from the two brain hemispheres, and to maintain or switch between behaviours. The central complex may provide inspiration for solving problems of conflict resolution between behavioural modules competing for control of a limited set of effectors. In vertebrate neuroscience, the basal ganglia has been associated with this problem of 'action selection' [110]—the central complex might have a similar function in insects. The central complex may also be involved in path integration, which requires the association of several modalities, in particular polarized light or other compass sensing, and visual or proprioceptive measures of distance. Some computational models of neural networks capable of path integration [111, 112] share features with the central complex, in particular rows of neural elements with specific columnar and global connection patterns [113].

The final and critical loop of our architecture is provided by efference copies of motor commands, which can in principle provide predictions of expected sensory events. This is vital contextual information for distinguishing external disturbances from reafference. Such mechanisms play a role in priming sensory systems, to anticipate and inhibit the sensory consequences of movements. In this way, an estimate of feedback can be compared to actual sensory feedback and thereby provide appropriate reinforcement for learning. State estimation can combine the model's prediction with sensory feedback, thereby allowing the evaluations of sensorimotor counterfactuals. Neural correlates of reward predictors exhibit different reward-related responses depending on whether rewards are expected [31]. Evidence suggests that similar reward-like reference signals also exist in mammalian brains [114, 115]. It is a very interesting question to determine the extent to which accurate prediction—which implies the use of forward models [74]—actually occurs in insect systems, and whether this might be an additional function implemented in the mushroom bodies or other specific neural centres.

5. Conclusion

Insects solve difficult behavioural tasks with miniature brains. We have reviewed the current state of neurobiological research on insect nervous systems to identify essential elements of their control architecture. Although much remains uncertain and speculative, nevertheless some interesting general features emerge. In particular, parallel direct sensorimotor loops (or 'behaviours') are supplemented by specific brain areas that serve integrative functions relating to context-dependence, learning, and smooth coordination. Moreover these areas have distinctive neural architectures, preserved across all insect species, that suggest particular ways in which these functions might be implemented. Attempting to copy these systems should be productive for robot research; and should also contribute to extending biological understanding of the organization of behaviour in insects [116, 117].

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