

COMMENTARY

Connecting brain to behaviour: a role for general purpose steering circuits in insect orientation?

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ABSTRACT

The lateral accessory lobes (LALs), paired structures that are homologous among all insect species, have been well studied for their role in pheromone tracking in silkmoths and phonotaxis in crickets, where their outputs have been shown to correlate with observed motor activity. Further studies have shown more generally that the LALs are crucial both for an insect's ability to steer correctly and for organising the outputs of the descending pathways towards the motor centres. In this context, we propose a framework by which the LALs may be generally involved in generating steering commands across a variety of insects and behaviours. Across different behaviours, we see that the LAL is involved in generating two kinds of steering: (1) search behaviours and (2) targeted steering driven by direct sensory information. Search behaviours are generated when the current behaviourally relevant cues are not available, and a well-described LAL subnetwork produces activity which increases sampling of the environment. We propose that, when behaviourally relevant cues are available, the LALs may integrate orientation information from several sensory modalities, thus leading to a collective output for steering driven by those cues. These steering commands are then sent to the motor centres, and an additional efference copy is sent back to the orientation-computing areas. In summary, we have taken known aspects of the neurophysiology and function of the insect LALs and generated a speculative framework that suggests how LALs might be involved in steering control for a variety of complex real-world behaviours in insects.

KEY WORDS: Lateral accessory lobe, Insect navigation, Orientation, Motor control, Central complex

Introduction

The behavioural repertoire of insects includes a variety of sensory-driven orientation behaviours (Heinze, 2017). At the reactive end of the spectrum, some stereotyped escape responses may be triggered by innate responses to species-specific cues – for instance, the predator-escape behaviour of cockroaches following detection of air vibrations (Camhi et al., 1978), the predator-escape behaviour of moths triggered by ultra-sound cues (Roeder, 1962) or, similarly, escape behaviours in locusts triggered by looming visual cues (O'Shea and Williams, 1974). In contrast, some orientation behaviours rely on multiple cues from the environment, which may have to be learned and may need to be acquired over several modalities. A few examples are straight-line orientation in dung beetles (el Jundi et al., 2015), long-distance migration in monarch butterflies (Reppert et al., 2004), and homing strategies in ants

(Muller and Wehner, 1988; Wehner and R  ber, 1979) and bees (Von Frisch, 1956).

In many insect species, orientation strategies have been investigated at a physiological level as well as at the behavioural level, thus providing some insights into how neural circuits underlie orientation. We can take these physiological findings and combine them with the results of computational modelling to begin to understand how particular circuitry in the brain can orchestrate the computations required for orientation behaviours (Ardin et al., 2016; Kottler et al., 2017preprint; Stone et al., 2017). However, these models often do not consider how specific motor areas are involved in producing behaviour (Fiore et al., 2017; Kottler et al., 2017, preprint), or how different orientation strategies interact. There are models of motor control that show how the motor system activates muscles and which motor behaviours can be executed (Collins and Stewart, 1993; Holmes et al., 2006; Pearson, 1993). However, there is a gap in our understanding of what happens between higher processing centres in the brain and subsequent motor control, and therefore how behavioural requirements are implemented. A deeper understanding of a particular structure in the insect brain, the lateral accessory lobes (LALs; see Glossary), may begin to fill this gap.

There is mounting anatomical and physiological evidence from across insect species that the LALs function as the major pre-motor area (Shih et al., 2015); they take input from several sensory modalities and higher processing centres (Namiki and Kanzaki, 2016) and give rise to neurons that project through the neck connective (see Glossary) to thoracic motor centres. The purpose of this Commentary is to propose a framework for understanding the role of the LALs in steering. In order to do this, we will begin by reviewing the available evidence for the involvement of the LAL in steering behaviours. In particular, we will relate the known neurophysiology of the LAL to the requirements of well-studied model behaviours. In doing so, we highlight general principles by which the highly conserved organisation of the LAL may play a role in a broad range of sensory-driven behaviours, including, we speculate, those that have not yet been subject to neurophysiological investigation. It is clear from previous work that the LALs are not simply the final relay stage in a chain that leads to steering movements. They are also involved in producing active sampling (see Glossary) behaviours that influence the sensory information that is acquired by an individual. Thus, we argue that a better understanding of these brain regions may well provide fresh insight into the fine motor details of insect behaviours across a variety of sensory ecologies.

LAL neuroanatomy is homologous across species

The LALs [or iDFP in *Drosophila* (Chiang et al., 2011) and ventral body in Diptera (Strausfeld and Li, 1999)] are paired neuropils (see Glossary) located in the medial protocerebrum of insects. They are located laterally to the central complex and are bordered by the

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Glossary**Active sampling**

Using movements to create, change or increase the quality of sensory input.

Bistable

A neuron or network of neurons having two possible stable states of activity.

Central pattern generator

A neural circuit that produces rhythmic outputs in the absence of rhythmic input.

Efference copy

An internal copy of a movement-producing signal that can be used to update internal models or predict the sensory consequences of movements.

Lateral accessory lobes (LALs)

Paired neuropils that are located in the medial protocerebrum of insect brains.

Neck connective

The structure resembling a neck in insects, connecting the head with the thorax.

Neuropil

A dense network of interwoven nerve fibres as well as their branches and synapses.

Path integration

Calculating one's current position in relation to a starting position by using estimates of speed and direction.

mushroom body (MB) lobes dorsally, and the antennal lobe frontally (Chen et al., 2018; see Fig. 1A), and seem to be homologous among insect species and perhaps also other arthropods (Thoen et al., 2017). Their connectivity suggests that they play an important role in motor coordination.

The LALs are located downstream of the sensory processing areas of the cerebrum, including the central complex (CX), but upstream of the motor control areas of the thoracic ganglia. The LALs are the major output region of the CX, which is thought to compute and monitor the heading of the individual within the environment; the CX is also involved in the control of orientation (Heinze and Homberg, 2009; Heinze et al., 2013; Homberg, 1985; Kanzaki et al., 1992; Lin et al., 2013). The LALs also receive a variety of other sensory inputs (Fig. 1B). These include inputs from a range of visual processing areas, such as the medulla, the lobula, the lobula plate (Namiki and Kanzaki, 2018) and the anterior optic tubercles (involved in the processing of polarised light; Heinze and Homberg, 2008). Olfactory inputs from the antennal lobes are transmitted to the LALs via the superior medial protocerebrum (Mishima and Kanzaki, 1999), and flight control-related inputs are sent from the motor centres (Homberg, 1994). The LALs receive additional inputs from the MBs (Aso et al., 2014; Manjila et al., 2019), higher brain areas responsible for learning (Ardin et al., 2016; Cassenaer and Laurent, 2007) and cognitive processing (Menzel and Giurfa, 2001) in complex orientation tasks, as demonstrated by their size correlating with the complexity of foraging tasks in social insect species (Bernstein and Bernstein, 1969; Farris and Schulmeister, 2011).

The inputs to each side of the LAL reflect the segregated way in which each hemisphere of the insect brain processes information (Paulk et al., 2015). That is, the inputs to one LAL overwhelmingly originate from the ipsilateral hemisphere, albeit there are some contralateral inputs carrying visual and olfactory information (Namiki et al., 2014; Namiki and Kanzaki, 2018). The outputs of the LALs mainly project downstream via the posterior slope (PS; thought to be another pre-motor centre) and ventral medial

protocerebrum towards wing and leg neuropils (Cande et al., 2018), with some projections also connecting upstream to the CX (Homberg, 1994), the superior medial protocerebrum (Namiki et al., 2014) and the visual processing areas (Namiki and Kanzaki, 2018; Namiki et al., 2014). Each LAL can be subdivided into the dorsal LAL (sometimes referred to as the outer LAL) and the ventral LAL (inner LAL). Namiki et al. (2014) found that the vast majority of inputs to LALs innervate the dorsal division and the vast majority of outputs project from the ventral division of the LAL.

The neurons originating in the LAL can be categorised into three major types (Fig. 2A,B), the organisation of which seems to be conserved across insects. The first type is a contralaterally descending neuron (Type I in the context of this Commentary), which takes dendritic inputs on the ipsilateral side of the upper LAL and projects to both the dorsal and ventral parts of the contralateral LAL, before continuing downstream to the PS and the thoracic ganglia. The second type is an ipsilaterally descending neuron (Type II), which innervates the dorsal and ventral division of the LAL, as well as the ventral protocerebrum (VPC), before continuing downstream towards the PS. The third kind of neuron originating in the LAL is a bilateral neuron (Type III), connecting the LALs of both hemispheres. For Type III neurons, the vast majority of dendritic inputs are located in the dorsal division of the ipsilateral LAL, whereas the vast majority of outputs are located in the ventral division of the contralateral LAL (Namiki et al., 2014). This class of neurons may be inhibitory (Iwano et al., 2010). All three neuron types usually project both their dendrites and axons throughout the entire division they innervate, and the pre-synaptic branches of innervating neurons do not seem to be separated into different regions for different sensory modalities of LAL input (Namiki et al., 2014).

LALs are involved in the generation of a range of orientation behaviours

The most extensively studied steering behaviour originating from the LAL is the pheromone-tracking behaviour of male silkmoths (*Bombyx mori*; Fig. 3A). The domestication of the silkmoth as part of the silk industry has led to the generation of large individuals that do not fly as well as their natural ancestors, and an interesting by-product of this is that the walking silkmoth makes an ideal model system for the study of pheromone tracking. Female silkmoths release pheromones that the male moths detect with their antennae and then track upwind (Olberg, 1983). This tracking behaviour follows a stereotypical pattern: first, the detection of the pheromone elicits a surge, where the moth turns towards the odour source and walks in a straight line. Second, when the pheromone is no longer detected, the moth starts zig-zagging (turning left and right in quick succession). Finally, this zig-zag phase terminates in a loop. However, if at any point during this sequence more packets of pheromones are detected, the moth resets to the surge behaviour. Thus, the degree of straightness in a moth's path will depend on the amount of pheromone, with search strategies naturally structured by the history of pheromone absence (Namiki et al., 2014; Pansopha et al., 2014).

Kanzaki and colleagues identified the LAL as being key to the generation of the observed zig-zag searching portion of the behaviour (Kanzaki and Shibuya, 1992). This pattern is thought to be generated together with the adjacent VPC (Iwano et al., 2010). The interaction between the LAL and VPC results in Type I neurons generating 'flip-flop' signals, which involve a repeating biphasic activity, consisting of periods of high and low firing rates (Kanzaki and Shibuya, 1992; Kanzaki et al., 1992; Mishima

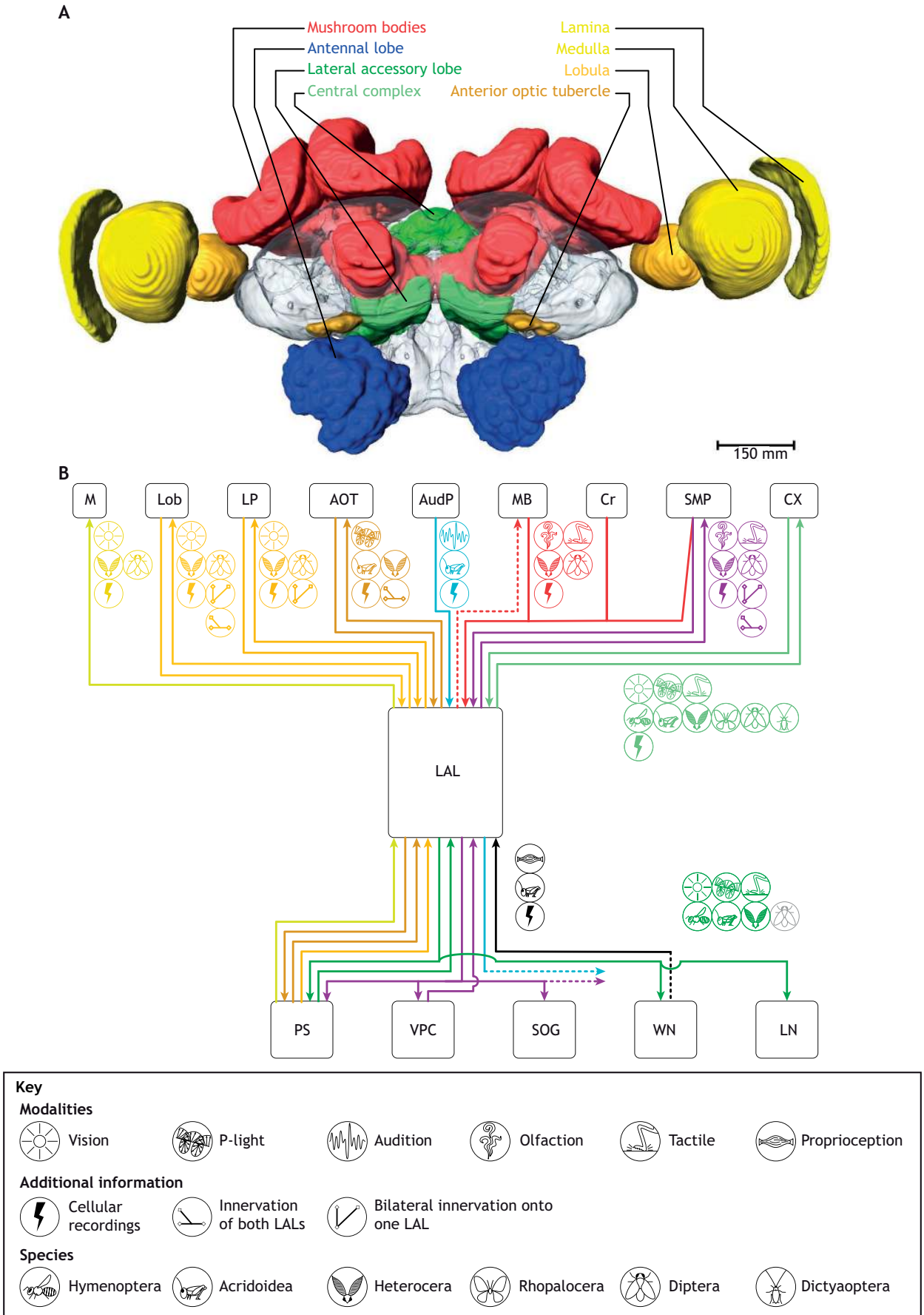


Fig. 1. See next page for legend.

Fig. 1. Brain organisation and lateral accessory lobe (LAL) connectivity. (A) A 3D render of the brain of the ant *Cataglyphis noda* (image reproduced with permission from Jens Habenstein and the Rössler Group in Würzburg). The major brain areas that are associated with the LAL are indicated. (B) Wiring diagram of the connections of the LAL from and to other brain areas. The figure shows how these connections compare across species and modalities. AOT, anterior optic tubercle; AudP, auditory pathway; Cr, crepine; CX, central complex; LN, leg neuropils; Lob, lobula; LP, lobula plate; M, medula; MB, mushroom body; P-light, polarised light; PS, posterior slope; SMP, superior medial protocerebrum; SOG, sub-oesophageal ganglia; VPC, ventral protocerebrum; WN, wing neuropils. The connectivity diagram comes from a literature review of known LAL connections and all references are given in the main text. The information regarding which species and which sensory modalities were studied is given by the pictograms and the key, and dotted lines and grey icons depict uncertain or suggested connections.

and Kanzaki, 1999). The firing activities of the Type I neurons from the two hemispheres are in anti-phase, with the ipsilateral flip-flop neuron in its upstate when the contralateral neuron is in its downstate, and the pattern switching regularly. The activities of these bistable (see Glossary) flip-flop neurons correlate strongly with motor output during pheromone-seeking behaviour (Iwano et al., 2010; Namiki and Kanzaki, 2016): when the descending neurons on one side are in a state of high activity, the neck motor neurons on the same side are activated, thus activating the neck muscles and initiating a turn. Furthermore, a neuron that is morphologically similar to these Type I flip-flop cells underlies some types of turn in the fruit fly (Schnell et al., 2017). We therefore suggest that it is likely that the LAL network creates the steering commands for the observed moth zig-zag searching behaviours.

In a different insect species, the cricket *Gryllus bimaculatus*, the LAL has been implicated in phonotaxis behaviour (Zorović and Hedwig, 2011; Fig. 3B). Male crickets produce stereotyped chirps, towards which female crickets turn in a reactive steering process. Again, as with moths, the activities of some classes of LAL neurons are correlated with the observed steering behaviour. Three types of neurons have been identified as being involved in phonotaxis, all of which appear to be morphologically and physiologically similar to the neurons found in the silkmoth (Fig. 2C). Ipsilateral descending neurons (Type II) respond more strongly when the sound source is located on the ipsilateral side, and the activity of Type II neurons also correlates with ipsilateral motor output. In contrast, the activity of contralaterally crossing (Type III) and descending (Type I) neurons correlates with contralateral motor outputs. Activating any of these neurons elicits the steering response predicted based on the observed correlation of neural activity and motor activity. Furthermore, inhibiting Type I neurons terminates walking activity altogether (Zorović and Hedwig, 2013).

Thus, although it is clear that the requirements of a cricket localising a sound source and a silkmoth searching for a pheromone source are very different, the two processes clearly share behavioural motifs and neural circuits (comparison in Fig. 2C). It is worth mentioning that state changes in Type I neurons can be elicited not only by pheromone input and acoustic signals but also by other sensory input such as light flashes (Olberg, 1983), showing that these neurons probably receive multimodal information. We therefore suggest that the LAL network can produce different orientation behaviours in different species of insect, depending on the specific ecological context of a species-specific behaviour.

The function of LAL neurons

From studies of pheromone tracking in silkmoths, it appears that the underlying architecture of zig-zag walking consists of the

contralaterally descending Type I neurons (Fig. 2) (Iwano et al., 2010; Namiki et al., 2014) that display patterns of flip-flop activity. However, this arrangement of Type I neurons is complex, with the LAL–VPC network implicated in providing periodic switching of hemispheric LAL activity. In this system, Type II neurons may connect the LAL with subdivisions of the VPC, while Type III neurons convey periodic inhibition between the two sides of the LAL (Iwano et al., 2010), facilitating the upstate/downstate pattern of activity between hemispheres.

Although the pheromone-tracking behaviour of the silkmoth provided early insights into LAL circuitry, it has since become clear that the same networks may also be involved in other behaviours in other insects, such as phonotaxis in the cricket (described above). Although the specific roles of LAL neuron types in cricket phonotaxis are not as well defined as for the zig-zag behaviour of silkmoths, it is the activity of Type I neurons that again best correlates with steering behaviour for walking (Zorović and Hedwig, 2011, 2013). Therefore, looking across these different behaviours, we see a general pattern that the contralaterally descending Type I neurons seem to be conveying the output of neural processing in the LAL network towards the thoracic ganglia; activity in Type I neurons therefore correlates with the motor output. Furthermore, if we consider the multimodality of this neuron type, it may be able to access signals from across sensory processing areas (Homberg, 1994; Iwano et al., 2010; Olberg, 1983) and thus provide a substrate for multi-modal cue arbitration or integration.

The idea that the LAL may be a location for signals from multiple sensory modalities to converge is supported by the known responses of LAL neurons across a variety of insects, suggesting that the LAL input area may be able to integrate signals. In locusts, LAL neurons involved in flight control are also sensitive to proprioceptive feedback and visual stimuli (Homberg, 1994). The LAL neurons involved in pheromone tracking in silkmoths are also sensitive to light (Kanzaki et al., 1994; Olberg, 1983) and optic flow (Pansophia et al., 2014). In crickets, LAL neurons that are sensitive to auditory cues are additionally sensitive to visual and mechanosensory stimuli (Zorović and Hedwig, 2013). In flies (Huston and Krapp, 2008; Schnell et al., 2017; Wertz et al., 2012), honeybees (Bidwell and Goodman, 1993; Goodman et al., 1987; Ibbotson et al., 2017) and locusts (Träger and Homberg, 2011), morphologically similar descending neurons have been found also. Some of these may originate in the LALs, while the others may belong to the PS. Generally, these are involved in optomotor control, but have been found to be sensitive to other sensory modalities. If this convergence is because the LAL plays a role in the integration of multi-modal information as it computes a unified output (i.e. the motor commands for steering), we can infer that the incoming information should share characteristics in the way that it relates to desired behaviour. That is, the incoming information should be of the same ‘unit’, with the most obvious units for this incoming information being simple turn or attraction/aversion signals, as has been suggested previously (Wolff and Strausfeld, 2015; Olberg, 1983; Wessnitzer and Webb, 2006). In order to optimally integrate turning signals, the inputs should also incorporate information on reliability, because the different sensory cues that lead to orientation information would have varying levels of accuracy (Wystrach et al., 2015). Therefore, we can propose two general functions of the LAL network: firstly, we propose that in the absence of task-specific sensory information, the LAL network acts as a generator of local random searching behaviour (Fig. 4), such as stochastic turns or casting; secondly, we propose that when task-relevant stimuli are

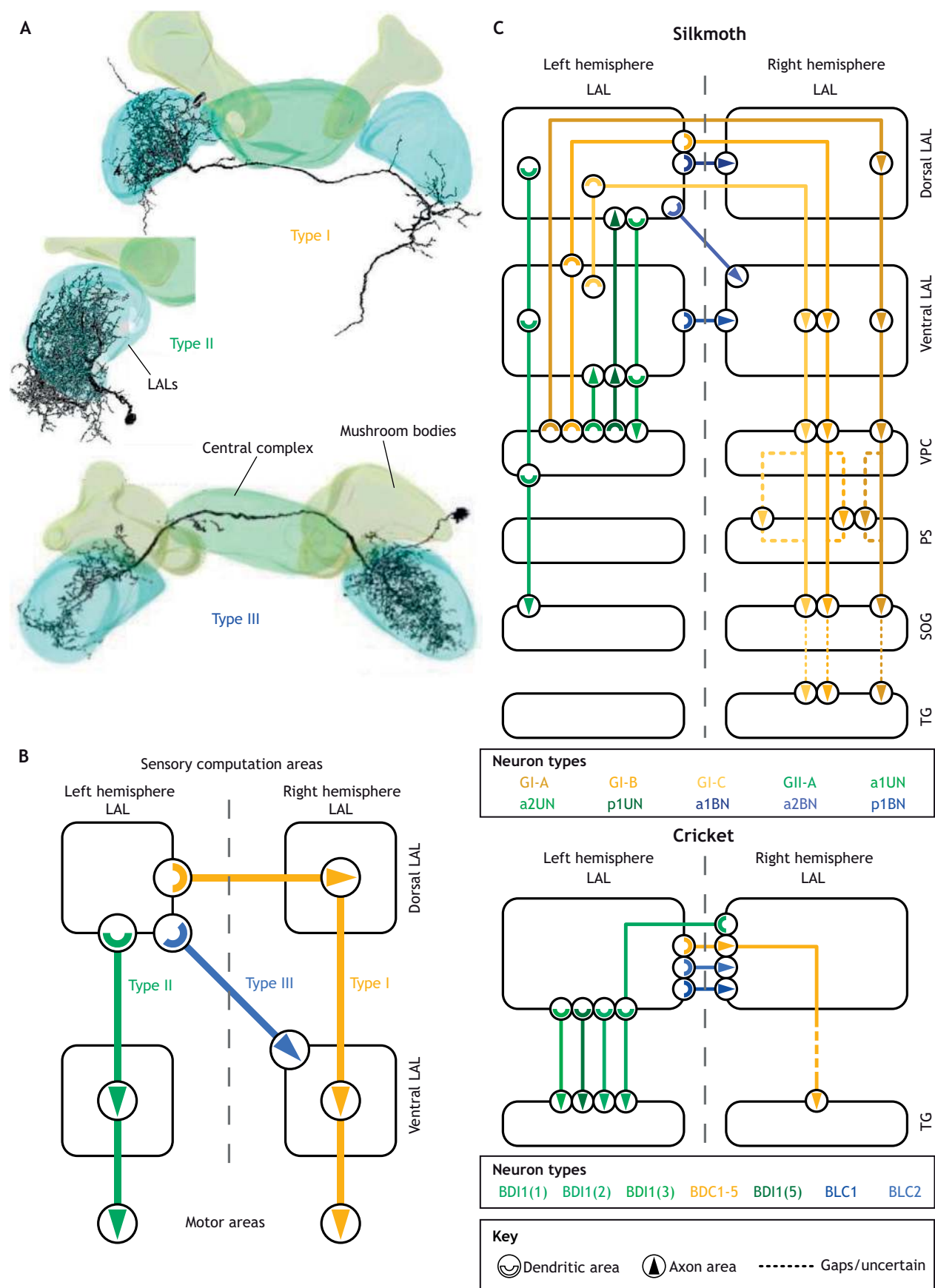


Fig. 2. See next page for legend.

Fig. 2. Neuron classes and connectivity within the LAL. (A) Neuroanatomy of the three representative neuron types found in the *Bombyx mori* (silkmoth) LAL. Neuron figures were taken from Namiki et al. (2014), with slight adaptations. Type I, contralaterally descending; Type II, unilaterally descending; Type III, bilaterally connecting. (B,C) Representative neuron connections originating in the left LAL. (B) The generalised schematic diagram of the basic connectivity of the three neuron types, originating in the left hemisphere, is based on data from silkmoth (*B. mori*) and cricket (*Gryllus bimaculatus*). (C) For silkmoth (top) and cricket (bottom), we show more detailed information on the known neuron types originating in the left hemisphere. Orange, subtypes of Type I neurons; green, subtypes of Type II neurons; blue, subtypes of Type III neurons; triangles, output from the neuron; half-circles, input to the neuron. Other neuron subtypes have been identified in moths, although their exact functions have not been determined yet, so they are not shown here. PS, posterior slope; SOG, sub-oesophageal ganglia; TG, thoracic ganglia; VPC, ventral protocerebrum.

available, the LAL network acts to integrate the available information in order to generate directed turns (Fig. 5).

The LAL: a general steering circuit?

Motivation for steering

Some organisms control their movement with kinesis mechanisms, in which they move away from unfavourable conditions in a stochastic manner and eventually, by chance, reach a spot that is more favourable. However, for the vast majority of navigation behaviours, steering is essential; this excludes kinesis behaviours, as steering is the process of deliberately changing one's orientation in response to sensory information or in order to improve the quality of incoming sensory information. For the purposes of this Commentary, we have divided the potential motivations for steering into three categories: reflexive turns, goal-directed searching behaviours and goal-directed targeting behaviours.

Reflexive behaviours are often triggered in the context of predator-escape responses. A few examples are the visual escape responses in locusts (O'Shea and Williams, 1974) and flies (von Reyn et al., 2017), the cerci of cockroaches detecting air movements caused by predators (Camhi et al., 1978), and moths detecting ultrasounds emitted by bats (Roeder, 1962). All of these behaviours can be elicited by direct connections to motor areas from a sensory processing region, although in some instances, nuances in the

escape behaviour (Card and Dickinson, 2008) suggest additional processing may occur.

Small-scale goal-directed searching behaviours are elicited when there is a specific goal, such as finding food, conspecifics or a nest, and when there is potentially a way of optimising one's movements to increase the chances of finding useful sensory information. Such search behaviours often appear to be rather similar, even when different modalities are involved. For example, one can compare the zig-zag walk of the silkmoth, which is driven by a search for pheromones, with the visual scanning behaviour of desert ants. In this scanning behaviour, ants remain at a single location but turn from side to side, sampling the visual scene at a variety of different orientations (Wystrach et al., 2014). Further examples would include the casting behaviour of a flying moth, again searching for pheromones, but also the 'dancing' of the dung beetle as it seeks a familiar compass orientation (Baird et al., 2012). All of these behaviours lead to an increased sampling of the environment and increase the likelihood of encountering useful sensory information (Fig. 4).

Goal-directed target steering is evoked when sensory cues associated with the current goal are available. This type of steering encompasses a range of taxis behaviours, such as the chemotaxis and phonotaxis discussed above, that are seen across the animal kingdom. The description 'goal-directed target steering' is also appropriate for behaviours that are classified as more complex than simple taxis behaviours. An example would be the visual guidance behaviours of bees or ants, which orient towards important objects to find food (Giurfa, 2007) or orient within visual scenes to find their way back to the nest (Zeil, 2012). In both cases, the orientation of the individual depends on learned information and cannot depend solely on hardwired sensory circuits. Furthermore, important behaviours, such as returning to a central nest location, rely on redundant mechanisms, and multiple orientation estimates need to be combined, as ants seem to do with path integration (see Glossary) and visual guidance (Collett, 2012; Hoinville and Wehner, 2018; Wehner et al., 2016). Thus, goal-directed steering in insects is likely to require multi-modal input from diverse brain areas, pulling together different modalities but also information derived from comparisons of current and learned sensory information (Fig. 5).

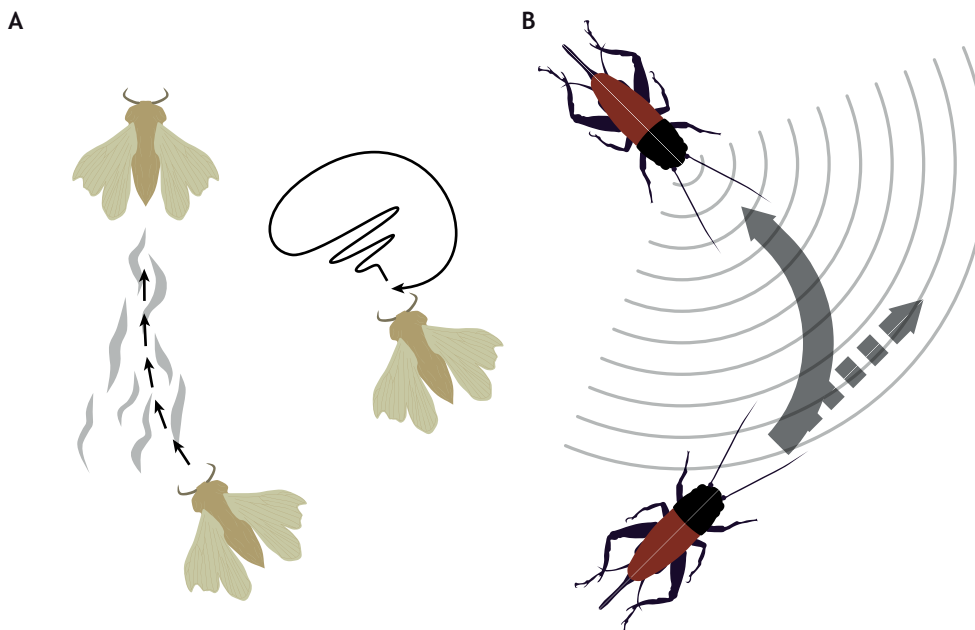


Fig. 3. LAL-mediated behaviours in silkmoth and cricket. (A) Pheromone-tracking behaviour in *B. mori* (silkmoth). When a walking moth perceives pheromone, it surges forward (left); when no more pheromone is detected, the moth performs a stereotypic zig-zag behaviour (right), which eventually leads to a full circling behaviour. If, at any point, more pheromone is detected, the sequence resets to the initial surge. (B) Phonotaxis in *G. bimaculatus* (cricket). Crickets perceiving a conspecific's call will turn towards the sound source and approach (solid arrow). The dashed arrow shows the ongoing trajectory, if the cricket had not received the stimulus. Together, the zig-zag and loop in A and the coordinated turn in B demonstrate examples of small-scale search as well as targeted steering; we propose these are the two types of steering required from LAL outputs.

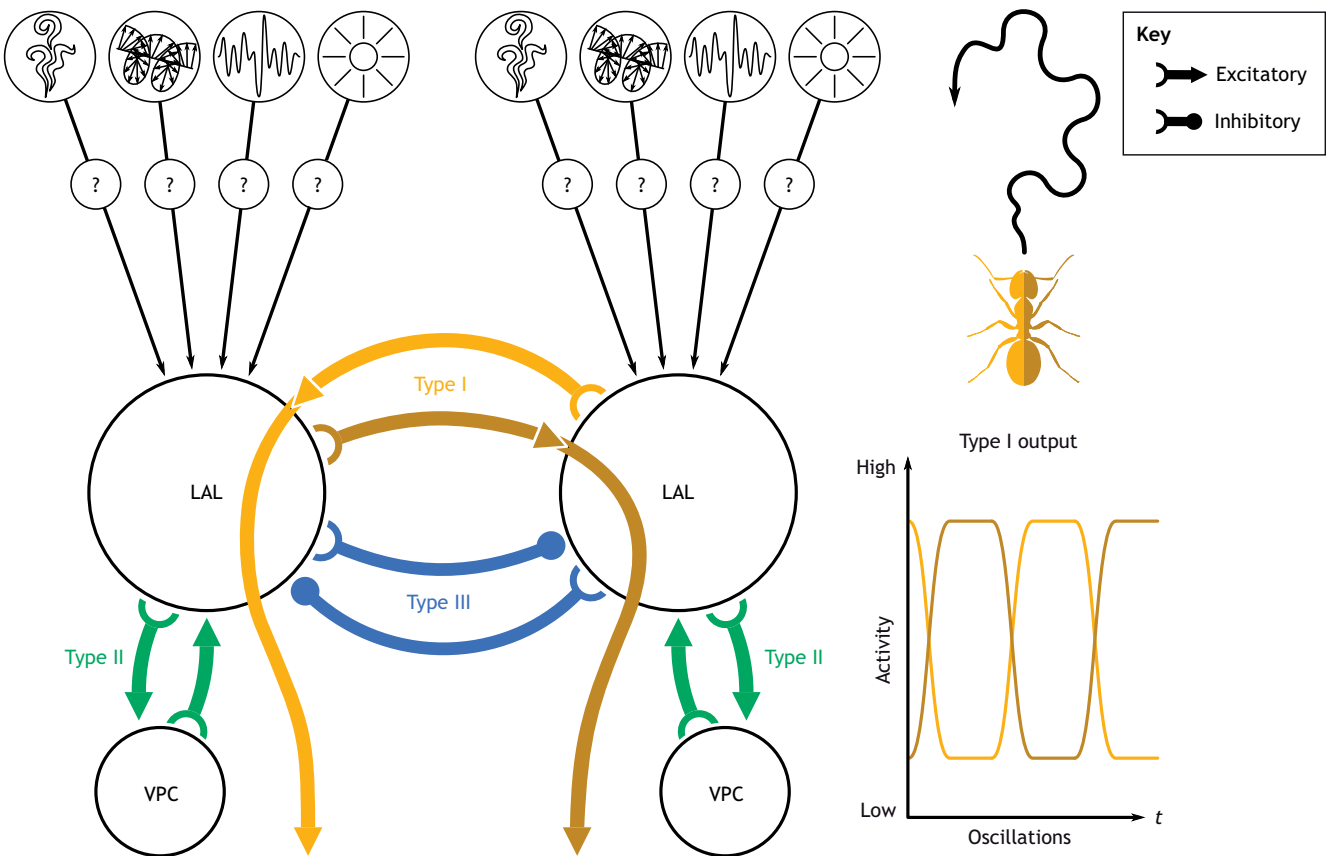


Fig. 4. A proposed LAL circuit for generating small-scale search behaviour. Task-relevant searching behaviour generated by the LAL–ventral protocerebrum (VPC) network would be initialised and generated when goal-relevant stimuli are not perceived (question marks indicate absence of stimuli). Type I neurons would represent the output of the local network of one hemisphere and project motor activity into the other hemisphere, with the activity of these neurons anti-phasically modulated (in a central pattern generator-like manner; see Glossary), therefore steering the agent from side to side. The output of this network would increase the sampling rate of potentially useful sensory stimuli. Triangles, output from the neuron; half-circles, input to the neuron.

The role of the LAL in controlling direction

The physical process of steering involves just a few necessary movement primitives: forward, left, right and (rarely) backwards. Therefore, the motor centre does not need to receive information about precisely where certain stimuli in the environment are located, it simply needs to be told which stereotypical motor programmes to execute at any point in time (D'Avella et al., 2015; Ijspeert, 2008; Land et al., 2013). Thus, at the level of the LAL output, and therefore the information received by motor centres, there may be organisation as simple as a Braitenberg vehicle (Braitenberg, 1984) or a tank; that is, the only information needed is the force to be executed by the left and right motors (this idea is discussed in more detail below). Exerting the same force direction on both sides will lead to forward motion, but if the forces are not equally directed, the resulting motion will be steering of some kind. Taking all of the above considerations together, we see that the requirements for a general steering circuit include: (i) integration of multiple orientation inputs; (ii) division of left and right in a computational sense; and (iii) generation of different output patterns.

The architecture of the LAL naturally has the appropriate qualities to meet these steering requirements: (i) it receives inputs from all brain areas that have been shown to be involved in the control of orientation behaviours; (ii) the LAL consists of paired neuropils, reflecting the hemispheric separation of turning information and descending pathways to the motor centres; and (iii) the outputs of each LAL neuropil have been shown to

correlate with (Iwano et al., 2010) and generate (Zorović and Hedwig, 2013) the motor activity which is observed on the contralateral side (Type I neurons descend contralaterally). Thus, the output of the LAL network may code for the forces to be generated by the motor centre (their amount and/or their direction); if the output of one LAL (i.e. left side) exceeds the output of the other LAL (i.e. right side), steering is induced towards the direction of the higher output (left). Thus, the imbalance of the outputs of the two sides of the LALs seems to code for the direction of exhibited forces of the motor system. A similar model of steering has also been used in CX modelling (Stone et al., 2017) and odour-tracking robots (Ando et al., 2013; Ando and Kanzaki, 2015). This relationship between the LAL output and the motor activity has been shown for both searching behaviours (Iwano et al., 2010) and goal-directed target steering (Zorović and Hedwig, 2013).

How might this Braitenberg-like meta-command structure feed into the insect motor system? In the spirit of the simple framework that we put forward in this Commentary, we make some observations. We know that the flip-flop neurons from the LAL interact with neck motor neurons (Kanzaki and Mishima, 1996) that control head direction, and that their activity precedes full-body turns in walking as well as flying insects (e.g. Land, 1973); this suggests a general role of LAL neurons in steering. Furthermore, the descending neurons of the LAL also innervate the wing and leg neuropils (Namiki et al., 2018). For a change of steering direction,

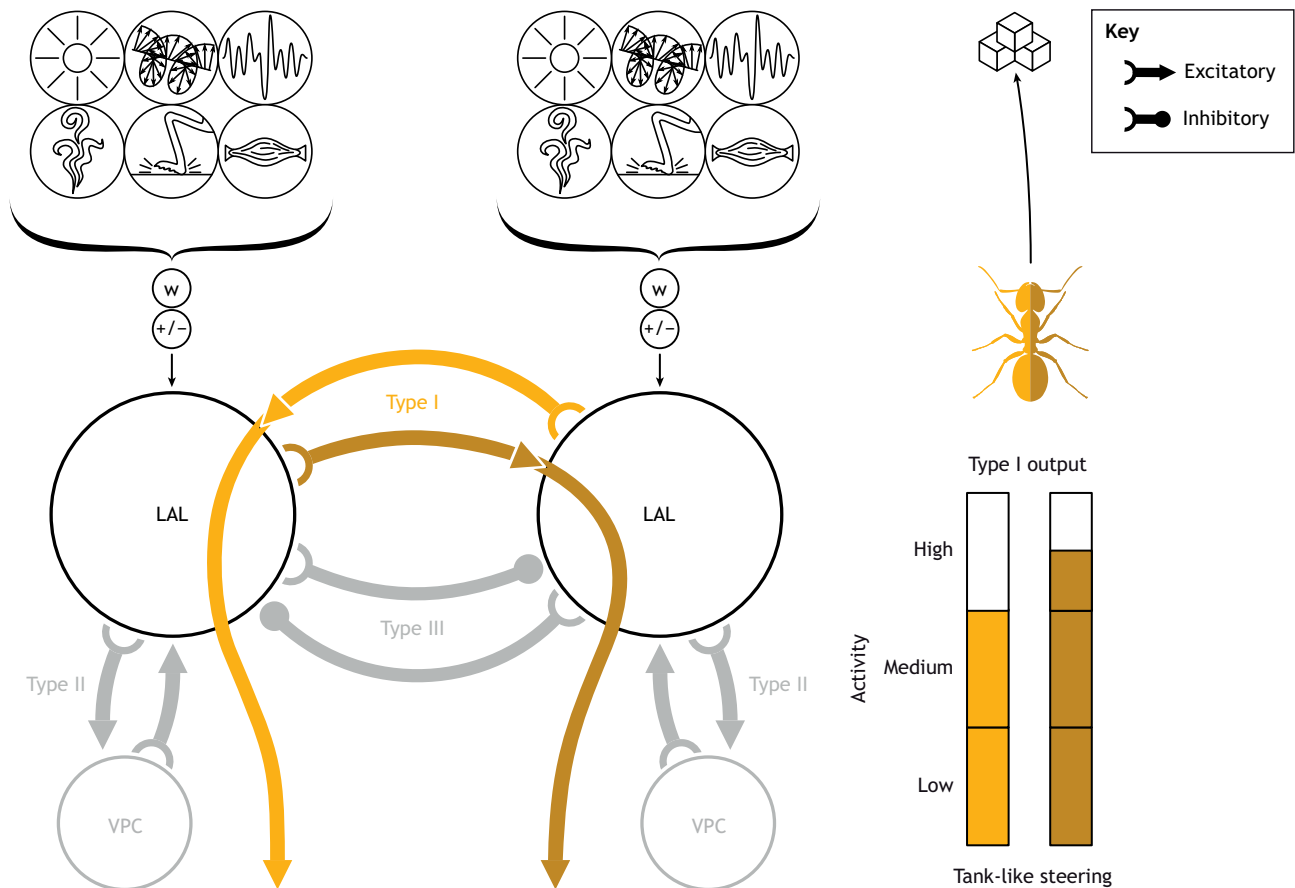


Fig. 5. A proposed LAL circuit for generating goal-directed turning. Goal-directed targeting behaviour generates steering commands towards a perceived goal. In this proposed model, the activity of Type I neurons is generated by the integration of turning inputs (w , weights; $+/-$, increased/decreased turning) from multiple modalities and navigation processes simultaneously, and for each hemisphere independently. Because Type I neurons descend contralaterally, the turning decisions of the left hemisphere would control the right motor centres. Thus, in our proposal, which necessarily represents a simplification of the real LAL circuitry, steering is a product of interhemispheric activity balance, analogous to a Braitenberg vehicle. Triangles, output from the neuron; half-circles, input to the neuron. Type II and III neurons are shown in grey because of a lack of data about how they are involved in goal-directed turning behaviour.

asymmetrical muscular activity on each side of the body is required (Bidwell and Goodman, 1993; Goodman, 1965); thus, if one side of the motor system has a strong turning command, an asymmetry has to be orchestrated with the other side. Leg coordination has been shown to have a strong decentralised component, with ‘leg controllers’ from each side sharing feedback (Bässler and Büeschges, 1998; D’Avella et al., 2015; Ritzmann and Zill, 2013; Schilling and Cruse, 2019preprint). Thus, the descending control signals that need to alter the thoracic motor pattern from walking to turning (Hellekes et al., 2011; Mu and Ritzmann, 2008) could be implemented by a decentralised structure. Furthermore, in this scheme, the output from the LAL would not have to code for the coordination of left and right activity, relying instead on decentralised organisation.

Another possibility is that the combination of the unilaterally descending neurons (Type II) and the contralaterally descending neurons (Type I) from the LAL or PS carries the required coordination signal. In honeybees, recordings of descending neurons have shown that the information carried on both sides has some symmetry (Goodman et al., 1987). Therefore, it is quite possible, albeit speculative, that if a certain turning strength and direction emerges on one side of the LAL, the accompanying turning signal could be transmitted via both Type I and Type II neurons simultaneously. Type III neurons could play a role in

coordinating the turning signals between sides, where if only one side is more strongly activated, it will automatically activate the contralateral neurons representing the same movement.

Asymmetric coordination works well for walking and should work well for flying as well. Roll and yaw could be coordinated in such a fashion, whereas pitch would need symmetrical control. Some of the descending neurons in the honeybee have been shown to innervate both sides of the motor system, while being sensitive to optic flow (Bidwell and Goodman, 1993). Therefore, the role of the LAL could be to convey voluntary steering commands for both walking and flying.

The crucial role of the LALs in steering has been confirmed in cockroaches. Harley and Ritzmann (2010) lesioned the MBs, several subdivisions of the CX and the LALs. Only when the LALs were lesioned did cockroaches completely fail to steer. Going further, the idea that the LALs produce simple steering output is also consistent with the results of Cande et al. (2018) and their mapping of the descending pathways in *Drosophila*. It was shown that several distinct classes of motor behaviour are coded in separate clusters of motor fibres that form the descending pathway. One of the major clusters is responsible for steering while walking and another is responsible for steering while flying. Although there is more to know with regard to interactions with the PS, in these descending pathways, the parsimonious framework for the involvement of

LALs in steering – as proposed in this Commentary – fits nicely with the broad results of Cande et al. (2018).

Efference copy

An additional useful feature of a steering framework is the ability to return efference copy (see Glossary) back to sensory and processing brain areas, a process thought to be crucial for dynamic interaction with an environment. It is therefore not a surprise to see that outputs of the LAL do feed back to the CX, visual processing areas and probably other brain areas as well (Fig. 1B; Homberg, 1994; Namiki and Kanzaki, 2018; Namiki et al., 2014; Olberg, 1983). Thus, LAL output can be used to predict expected sensory changes as a function of turning, e.g. visual areas should receive information about expected optic flow signals (Webb, 2004), as seems to be the case in *Drosophila*, where lobula plate cells receive ascending inputs that accurately predict optic flow (Kim et al., 2015). These efference copies precede the activation of motor areas, and the signals are matched to the sign and magnitude of expected turns, as would be expected if the efference copy was an output of the LAL. Indeed, the occurrence of an efference copy related to the LAL has been suggested in the pheromone-tracking behaviour of moths (Pansopha et al., 2014). In that study, moths were presented with external optic flow information during the zig-zag phase of their pheromone-tracking behaviour. Moths ignore optic flow that does not match their expected optic flow direction, but when the presented optic flow matches expected flow direction, but is altered in magnitude, zig-zag turns are modulated in size. Clearly, there is an interaction between visual processing and the generation of this steering behaviour, which is consistent with a role for efference copy from the LAL. Indeed there is anatomical evidence connecting the visual processing areas with the LALs (Heinze, 2017; Namiki, et al., 2014; Namiki and Kanzaki, 2018). Furthermore, other processing areas, such as the CX, also receive feedback from the LAL (Heinze, 2015; Homberg, 1994). Thus, it may be effective to generate efference copies of steering commands during LAL processing, and feed these back to other processing areas.

Conclusions and implications

Steering is a vital component of all behaviour, and understanding how sensory information from the real world drives steering is of fundamental interest not only in behavioural biology but also in sensory ecology and biomimetic engineering. Towards this end, in this Commentary we have reviewed literature on the neurophysiology of the LALs and their involvement in insect orientation. By filling in some gaps with reasoned speculation we have been able to propose a general framework of insect steering and how it could be implemented. The important insect brain regions are the LALs, which are situated downstream of the sensory processing areas and upstream of thoracic motor centres. Thus, they are ideally located to translate orientation decisions from navigational computations into steering signals for the motor centres. The evidence from detailed studies of pheromone tracking in moths and phonotaxis in crickets, alongside supplemental evidence from other insects, suggests that the LALs could be involved in generating steering signals for small-scale searching behaviours, as well as integrating orientation decisions from a range of brain areas in order to control goal-directed locomotion. Consistent with this idea, the anatomical layout of the local LAL neurons, as well as their activity and input profiles are well suited to produce the appropriate motor patterns. This dual functionality of the LAL in steering behaviours is the basis for our proposal of a general steering framework dependent on the structure and function

of the LAL and our suggestion that this could underpin a broad range of species-specific sensory-driven behaviours in insects.

We hope that the general steering framework that we have proposed here can be useful in interpreting the behaviour of insects engaged in complex sensorimotor behaviours, where neurophysiological work is challenging or impossible (Namiki and Kanzaki, 2016). For instance, during the visual navigation of individually foraging ants, we see phases of searching for sensory information and goal-directed target steering. Ants with access to reliable visual information will travel smoothly along familiar routes; however, in the absence of reliable information, ants will modulate their motor patterns to increase sinuosity and then will eventually cease walking altogether and scan the surroundings to find familiar visual cues (Wystrach et al., 2014; Wystrach et al., 2019). Similar motor patterns are also seen in path integration-driven search (Wehner and Srinivasan, 1981) and in the zig-zag flight of wasps looking for their nest (Stürzl et al., 2016); thus, it is worth exploring whether the underlying neural networks are also shared. Because complex behaviours like navigation are difficult or impossible to recreate within the constraints of physiological experiments, it may be fruitful to also make use of computational modelling taking into account these ideas on steering. More generally, we hope that thinking about the nature of steering across insects will open up new paths for investigating the broadest range of orientation behaviours in a comparative manner.

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Competing interests

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References

- Ando, N. and Kanzaki, R. (2015). A simple behaviour provides accuracy and flexibility in odour plume tracking - the robotic control of sensory-motor coupling in silkworms. *J. Exp. Biol.* **218**, 3845–3854. doi:10.1242/jeb.124834
- Ando, N., Emoto, S. and Kanzaki, R. (2013). Odour-tracking capability of a silkworm driving a mobile robot with turning bias and time delay. *Bioinspir. Biomimet.* **8**, 016008. doi:10.1088/1748-3182/8/1/016008
- Ardin, P., Peng, F., Mangan, M., Lagogiannis, K. and Webb, B. (2016). Using an insect mushroom body circuit to encode route memory in complex natural environments. *PLoS Comput. Biol.* **12**, 1–22. doi:10.1371/journal.pcbi.1004683
- Aso, Y., Hattori, D., Yu, Y., Johnston, R. M., Iyer, N. A., Ngo, T.-T. B., Dionne, H., Abbott, L. F., Axel, R., Tanimoto, H. et al. (2014). The neuronal architecture of the mushroom body provides a logic for associative learning. *eLife* **3**, e04577. doi:10.7554/eLife.04577
- Baird, E., Byrne, M. J., Smolka, J., Warrant, E. J. Dacke, M. (2012). The dung beetle dance: an orientation behaviour? *PLoS ONE* **7**, e30211. doi:10.1371/journal.pone.0030211
- Bässler, U. and Büschges, A. (1998). Pattern generation for stick insect walking movements—multisensory control of a locomotor program. *Brain Res. Rev.* **27**, 65–88. doi:10.1016/S0165-0173(98)00006-X
- Bernstein, S. and Bernstein, R. A. (1969). Relationships between foraging efficiency and the size of the head and component brain and sensory structures in the red wood ant. *Brain Res.* **16**, 85–104. doi:10.1016/0006-8993(69)90087-0
- Bidwell, N. J. and Goodman, L. J. (1993). Possible functions of a population of descending neurons in the honeybee's visuo-motor pathway. *Apidologie* **24**, 333–354. doi:10.1051/apido:19930311
- Braitenberg, V. (1984). *Vehicles*. Cambridge, MA: MIT Press.
- Camhi, J. M., Tom, W. and Volman, S. (1978). The escape behavior of the cockroach *Periplaneta americana*. *J. Comp. Physiol.* **128**, 203–212. doi:10.1007/BF00656853
- Cande, J., Namiki, S., Qiu, J., Korff, W., Card, G. M., Shaevez, J. W., Stern, D. L. and Berman, G. J. (2018). Optogenetic dissection of descending behavioral control in *Drosophila*. *eLife* **7**, e34275. doi:10.7554/eLife.34275

- Card, G. and Dickinson, M. H. (2008). Visually mediated motor planning in the escape response of *Drosophila*. *Curr. Biol.* **18**, 1300–1307. doi:10.1016/j.cub.2008.07.094
- Cassenaer, S. and Laurent, G. (2007). Hebbian STDP in mushroom bodies facilitates the synchronous flow of olfactory information in locusts. *Nature* **448**, 709–713. doi:10.1038/nature05973
- Chen, C. L., Hermans, L., Viswanathan, M. C., Fortun, D., Aymanns, F., Unser, M., Cammarato, A., Dickinson, M. H. and Ramdya, P. (2018). Imaging neural activity in the ventral nerve cord of behaving adult *Drosophila*. *Nature Commun.* **9**, 1–10. doi:10.1038/s41467-018-06857-z
- Chiang, A.-S., Lin, C.-Y., Chuang, C.-C., Chang, H.-M., Hsieh, C.-H., Yeh, C.-W., Shih, C.-T., Wu, J.-J., Wang, G.-T., Chen, Y.-C. et al. (2011). Three-dimensional reconstruction of brain-wide wiring networks in *Drosophila* at single-cell resolution. *Curr. Biol.* **21**, 1–11. doi:10.1016/j.cub.2010.11.056
- Collett, M. (2012). How navigational guidance systems are combined in a desert ant. *Curr. Biol.* **22**, 927–932. doi:10.1016/j.cub.2012.03.049
- Collins, J. J. and Stewart, I. (1993). Hexapodal gaits and coupled nonlinear oscillator models. *Biol. Cybern.* **68**, 287–298. doi:10.1007/BF00201854
- D'Avella, A., Giese, M., Ivanenko, Y. P., Schack, T. and Flash, T. (2015). Modularity in motor control from muscle synergies to cognitive action representation. *Front. Comput. Neurosci.* **9**, 126. doi:10.3389/fncom.2015.00126
- el Jundi, B., Warrant, E. J., Byrne, M. J., Khaldy, L., Baird, E., Smolka, J. and Dacke, M. (2015). Neural coding underlying the cue preference for celestial orientation. *Proc. Natl. Acad. Sci. USA* **112**, 11395–11400. doi:10.1073/pnas.1501272112
- Farris, S. M. and Schulmeister, S. (2011). Parasitoidism, not sociality, is associated with the evolution of elaborate mushroom bodies in the brains of hymenopteran insects. *Proc. R. Soc. B Biol. Sci.* **278**, 940–951. doi:10.1098/rspb.2010.2161
- Fiore, V. G., Kottler, B., Gu, X. and Hirth, F. (2017). In silico interrogation of insect central complex suggests computational roles for the ellipsoid body in spatial navigation. *Front. Behav. Neurosci.* **11**, 142. doi:10.3389/fnbeh.2017.00142
- Giurfa, M. (2007). Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **193**, 801–824. doi:10.1007/s00359-007-0235-9
- Goodman, L. J. (1965). The role of certain optomotor reactions in regulating stability in the rolling plane during flight in the desert locust. *J. Exp. Biol.* **42**, 385–407.
- Goodman, L. J., Fletcher, W. A., Guy, R. G. and Mobbs, P. G. (1987). Motion sensitive descending interneurons, ocellar LD neurons and neck motoneurons in the bee: a neural substrate for visual course control in *Apis mellifera*. In *Neurobiology and Behaviour of Honeybees* (R. Menzel and A. Mercer), pp. 158–172. Springer Verlag.
- Harley, C. M. and Ritzmann, R. E. (2010). Electrolytic lesions within central complex neuropils of the cockroach brain affect negotiation of barriers. *J. Exp. Biol.* **213**, 2851–2864. doi:10.1242/jeb.042499
- Heinze, S. (2015). Neuroethology: unweaving the senses of direction. *Curr. Biol.* **25**, R1034–R1037. doi:10.1016/j.cub.2015.09.003
- Heinze, S. (2017). Unraveling the neural basis of insect navigation. *Curr. Opin. Insect Sci.* **24**, 58–67. doi:10.1016/j.cois.2017.09.001
- Heinze, S. and Homberg, U. (2008). Neuroarchitecture of the central complex of the desert locust: Intrinsic and columnar neurons. *J. Comp. Neurol.* **511**, 454–478. doi:10.1002/cne.21842
- Heinze, S. and Homberg, U. (2009). Linking the input to the output: new sets of neurons complement the polarization vision network in the Locust Central Complex. *J. Neurosci.* **29**, 4911–4921. doi:10.1523/JNEUROSCI.0332-09.2009
- Heinze, S., Florman, J., Asokaraj, S., El Jundi, B. and Reppert, S. M. (2013). Anatomical basis of sun compass navigation II: The neuronal composition of the central complex of the monarch butterfly. *J. Comp. Neurol.* **521**, 267–298. doi:10.1002/cne.23214
- Hellekes, K., Blincow, E., Hoffmann, J. and Büschges, A. (2011). Control of reflex reversal in stick insect walking: effects of intersegmental signals, changes in direction, and optomotor-induced turning. *J. Neurophysiol.* **107**, 239–249. doi:10.1152/jn.00718.2011
- Hoinville, T. and Wehner, R. (2018). Optimal multiguide integration in insect navigation. *Proc. Natl. Acad. Sci. USA* **115**, 2824–2829. doi:10.1073/pnas.1721668115
- Holmes, P., Full, R. J., Koditschek, D. and Guckenheimer, J. (2006). The dynamics of legged locomotion: Models, analyses, and challenges. *SIAM Rev.* **48**, 207–304. doi:10.1137/S0036144504445133
- Homberg, U. (1985). Interneurons of the central complex in the bee brain (*Apis mellifera*, L.). *J. Insect Physiol.* **31**, 251–264. doi:10.1016/0022-1910(85)90127-1
- Homberg, U. (1994). Flight-correlated activity changes in neurons of the lateral accessory lobes in the brain of the locust *Schistocerca gregaria*. *J. Comp. Physiol. A* **175**, 597–610. doi:10.1007/BF00199481
- Huston, S. J. and Krapp, H. G. (2008). Visuomotor transformation in the fly gaze stabilization system. *PLoS Biol.* **6**, e173. doi:10.1371/journal.pbio.0060173
- Ibbotson, M. R., Hung, Y.-S., Meffin, H., Boeddeker, N. and Srinivasan, M. V. (2017). Neural basis of forward flight control and landing in honeybees. *Sci. Rep.* **7**, 14591. doi:10.1038/s41598-017-14954-0
- Ijspeert, A. J. (2008). Central pattern generators for locomotion control in animals and robots: A review. *Neural Netw.* **21**, 642–653. doi:10.1016/j.neunet.2008.03.014
- Iwano, M., Hill, E. S., Mori, A., Mishima, T., Mishima, T., Ito, K. and Kanzaki, R. (2010). Neurons associated with the flip-flop activity in the lateral accessory lobe and ventral protocerebrum of the silkworm moth brain. *J. Comp. Neurol.* **518**, 366–388. doi:10.1002/cne.22224
- Kanzaki, R. and Mishima, T. (1996). Pheromone-Triggered 'Flipflop' neural signals correlate with activities of neck motor neurons of a male moth, *Bombyx mori*. *Zool. Sci.* **13**, 79–87. doi:10.2108/zsj.13.79
- Kanzaki, R. and Shibuya, T. (1992). Long-lasting excitation of protocerebral bilateral neurons in the pheromone-processing pathways of the male moth *Bombyx mori*. *Brain Res.* **587**, 211–215. doi:10.1016/0006-8993(92)90999-P
- Kanzaki, R., Sugi, N. and Shibuya, T. (1992). Self-generated zigzag turning of *Bombyx-Mori* males during pheromone-mediated upwind walking. *Zoolog. Sci.* **9**, 515–527.
- Kanzaki, R., Ikeda, A. and Shibuya, T. (1994). Morphological and physiological properties of pheromone-triggered flipflop descending interneurons of the male silkworm moth, *Bombyx mori*. *J. Comp. Physiol. A* **175**, 1–14. doi:10.1007/BF00217431
- Kim, A. J., Fitzgerald, J. K. and Maimon, G. (2015). Cellular evidence for efference copy in *Drosophila* visuomotor processing. *Nat. Neurosci.* **18**, 1247–1255. doi:10.1038/nn.4083
- Kottler, B., Fiore, V. G., Ludlow, Z. N., Buhl, E., Vinatier, G., Faville, R., Diaper, D. C., Stepto, A., Dearlove, J., Adachi, Y. et al. (2017). A lineage-related reciprocal inhibition circuitry for sensory-motor action selection. *bioRxiv*, 100420.
- Land, M. F. (1973). Head movements of flies during visually guided flight. *Nature* **243**, 299–300. doi:10.1038/243299a0
- Land, W. M., Volchenkov, D., Blaesing, B. E. and Schack, T. (2013). From action representation to action execution: exploring the links between cognitive and biomechanical levels of motor control. *Front. Comput. Neurosci.* **7**, 127. doi:10.3389/fncom.2013.00127
- Lin, C.-Y., Chuang, C.-C., Hua, T.-E., Chen, C.-C., Dickson, B. J., Greenspan, R. J. and Chiang, A.-S. (2013). A comprehensive wiring diagram of the protocerebral bridge for visual information processing in the *Drosophila* brain. *Cell Rep.* **3**, 1739–1753. doi:10.1016/j.celrep.2013.04.022
- Manjila, S. B., Kuruvilla, M., Ferveur, J.-F., Sane, S. P. and Hasan, G. (2019). Extended flight bouts require disinhibition from GABAergic Mushroom Body neurons. *Curr. Biol.* **29**, 283–293.e5. doi:10.1016/j.cub.2018.11.070
- Menzel, R. and Giurfa, M. (2001). Cognitive architecture of a mini-brain the honeybee. *Trends Cogn. Sci.* **5**, 62–71. doi:10.1016/S1364-6613(00)01601-6
- Mishima, T. and Kanzaki, R. (1999). Physiological and morphological characterization of olfactory descending interneurons of the male silkworm moth, *Bombyx mori*. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **184**, 143–160. doi:10.1007/s003590050314
- Mu, L. and Ritzmann, R. E. (2008). Interaction between descending input and thoracic reflexes for joint coordination in cockroach: I. descending influence on thoracic sensory reflexes. *J. Comp. Physiol.* **194**, 283–298. doi:10.1007/s00359-007-0307-x
- Muller, M. and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287–5290. doi:10.1073/pnas.85.14.5287
- Namiki, S. and Kanzaki, R. (2016). The neurobiological basis of orientation in insects: insights from the silkworm mating dance. *Curr. Opin. Insect Sci.* **15**, 16–26. doi:10.1016/j.cois.2016.02.009
- Namiki, S. and Kanzaki, R. (2018). Morphology of visual projection neurons supplying premotor area in the brain of the silkworm *Bombyx mori*. *Cell Tissue Res.* **374**, 497–515. doi:10.1007/s00441-018-2892-0
- Namiki, S., Iwabuchi, S., Pansopha Kono, P. and Kanzaki, R. (2014). Information flow through neural circuits for pheromone orientation. *Nat. Commun.* **5**, 5919. doi:10.1038/ncomms6919
- Namiki, S., Wada, S. and Kanzaki, R. (2018). Descending neurons from the lateral accessory lobe and posterior slope in the brain of the silkworm *Bombyx mori*. *Sci. Rep.* **8**, 9663. doi:10.1038/s41598-018-27954-5
- Olberg, R. M. (1983). Pheromone-triggered flip-flop interneurons in the ventral nerve cord of the silkworm moth, *Bombyx mori*. *J. Comp. Physiol. A* **152**, 297–307. doi:10.1007/BF00606236
- O'Shea, M. and Williams, J. L. D. (1974). The anatomy and output connection of a locust visual interneurone; the lobular giant movement detector (LGMD) neurone. *J. Comp. Physiol.* **91**, 257–266. doi:10.1007/BF00698057
- Pansopha, P., Ando, N. and Kanzaki, R. (2014). Dynamic use of optic flow during pheromone tracking by the male silkworm, *Bombyx mori*. *J. Exp. Biol.* **217**, 1811–1820. doi:10.1242/jeb.090266
- Paulk, A. C., Kirszenblat, L., Zhou, Y. and van Swinderen, B. (2015). Closed-loop behavioral control increases coherence in the fly brain. *J. Neurosci.* **35**, 10304–10315. doi:10.1523/JNEUROSCI.0691-15.2015
- Pearson, K. G. (1993). Common principles of motor control in vertebrates and invertebrates. *Ann. Rev. Neurosci.* **16**, 265–297. doi:10.1146/annurev.ne.16.030193.001405
- Reppert, S. M., Zhu, H. and White, R. H. (2004). Polarized light helps Monarch Butterflies navigate. *Curr. Biol.* **14**, 155–158. doi:10.1016/j.cub.2003.12.034
- Ritzmann, R. E. and Zill, S. N. (2013). Neuroethology of insect walking. *Scholarpedia* **8**, 30879. doi:10.4249/scholarpedia.30879

- Roeder, K. D. (1962). The behaviour of free flying moths in the presence of artificial ultrasonic pulses. *Anim. Behav.* **10**, 300–302. doi:10.1016/0003-3472(62)90053-2
- Schilling, M. and Cruse, H. (2019). Decentralized control of insect walking: a simple neural network explains a wide range of behavioural and neurophysiological results. *bioRxiv*, 695189. doi:10.1101/695189
- Schnell, B., Ros, I. G. and Dickinson, M. H. (2017). A descending neuron correlated with the rapid steering maneuvers of flying *Drosophila*. *Curr. Biol.* **27**, 1200–1205. doi:10.1016/j.cub.2017.03.004
- Shih, C.-T., Sporns, O., Yuan, S.-L., Su, T.-S., Lin, Y.-J., Chuang, C.-C., Wang, T.-Y., Lo, C.-C., Greenspan, R. J. and Chiang, A.-S. (2015). Connectomics-based analysis of information flow in the *Drosophila* brain. *Curr. Biol.* **25**, 1249–1258. doi:10.1016/j.cub.2015.03.021
- Stone, T., Webb, B., Adden, A., Weddig, N. B., Honkanen, A., Templin, R., Wcislo, W., Scimeca, L., Warrant, E. and Heinze, S. (2017). An anatomically constrained model for path integration in the bee brain. *Curr. Biol.* **27**, 3069–3085.e11. doi:10.1016/j.cub.2017.08.052
- Strausfeld, N. J. and Li, Y. (1999). Organization of olfactory and multimodal afferent neurons supplying the calyx and pedunculus of the cockroach mushroom bodies. *J. Comp. Neurol.* **409**, 603–625. doi:10.1002/(SICI)1096-9861(19990712)409:4<603::AID-CNE7>3.0.CO;2-P
- Stürzl, W., Zeil, J., Boeddeker, N. and Hemmi, J. M. (2016). How wasps acquire and use views for homing. *Curr. Biol.* **26**, 470–482. doi:10.1016/j.cub.2015.12.052
- Thoen, H. H., Marshall, J., Wolff, G. H. and Strausfeld, N. J. (2017). Insect-like organization of the stomatopod central complex: Functional and phylogenetic implications. *Front. Behav. Neurosci.* **11**, 1–18. doi:10.3389/fnbeh.2017.00012
- Träger, U. and Homberg, U. (2011). Polarization-sensitive descending neurons in the locust: connecting the brain to thoracic ganglia. *J. Neurosci.* **31**, 2238–2247. doi:10.1523/JNEUROSCI.3624-10.2011
- Von Frisch, K. (1956). The “Language” and orientation of bees. *Am. Philos. Soc.* **100**, 515–519.
- von Reyn, C. R., Nern, A., Williamson, W. R., Breads, P., Wu, M., Namiki, S. and Card, G. M. (2017). Feature integration drives probabilistic behavior in the *Drosophila* escape response. *Neuron* **94**, 1190–1204.e6. doi:10.1016/j.neuron.2017.05.036
- Webb, B. (2004). Neural mechanisms for prediction: Do insects have forward models? *Trends Neurosci.* **27**, 278–282. doi:10.1016/j.tins.2004.03.004
- Wehner, R. and Rüber, F. (1979). Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* **35**, 1569–1571. doi:10.1007/BF01953197
- Wehner, R. and Srinivasan, M. V. (1981). Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol. A* **142**, 315–338. doi:10.1007/BF00605445
- Wehner, R., Hoinville, T., Cruse, H. and Cheng, K. (2016). Steering intermediate courses: desert ants combine information from various navigational routines. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **202**, 459–472. doi:10.1007/s00359-016-1094-z
- Wertz, A., Haag, J. and Borst, A. (2012). Integration of binocular optic flow in cervical neck motor neurons of the fly. *J. Comp. Physiol. A* **198**, 655–668. doi:10.1007/s00359-012-0737-y
- Wessnitzer, J. and Webb, B. (2006). Multimodal sensory integration in insects—towards insect brain control architectures. *Bioinspir. Biomim.* **1**, 63–75. doi:10.1088/1748-3182/1/3/001
- Wolff, G. H. and Strausfeld, N. J. (2015). The insect brain: a commented primer. In *Structure and Evolution of Invertebrate Nervous Systems* (ed. A. Schmidt-Rhaesa, S. Harzsch and G. Purschke), pp. 597–639. Oxford University Press. doi:10.1093/acprof:oso/9780199682201.003.0047
- Wystrach, A., Philippides, A., Aurejac, A., Cheng, K. and Graham, P. (2014). Visual scanning behaviours and their role in the navigation of the Australian desert ant *Melophorus bagoti*. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **200**, 615–626. doi:10.1007/s00359-014-0900-8
- Wystrach, A., Mangan, M. and Webb, B. (2015). Optimal cue integration in ants. *Proc. R. Soc. B Biol. Sci.* **282**, 20151484. doi:10.1098/rspb.2015.1484
- Wystrach, A., Schwarz, S., Graham, P. and Cheng, K. (2019). Running paths to nowhere: repetition of routes shows how navigating ants modulate online the weights accorded to cues. *Anim. Cogn.* **22**, 213–222. doi:10.1007/s10071-019-01236-7
- Zeil, J. (2012). Visual homing: an insect perspective. *Curr. Op. Neurobiol.* **22**, 285–293.
- Zorović, M. and Hedwig, B. (2011). Processing of species-specific auditory patterns in the cricket brain by ascending, local, and descending neurons during standing and walking. *J. Neurophysiol.* **105**, 2181–2194. doi:10.1152/jn.00416.2010
- Zorović, M. and Hedwig, B. (2013). Descending brain neurons in the cricket *Gryllus bimaculatus* (de Geer): auditory responses and impact on walking. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **199**, 25–34. doi:10.1007/s00359-012-0765-7