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DOCTORAL THESIS

Biomimetic models of visual navigation - active sensing for embodied intelligence

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

in the

Insect Navigation Group

School of Life Sciences and Informatics

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Glossary

- Active sampling Using movements to create, change or increase the quality of sensory input. 78, 102, 116
- **Covariance** A measure of the joint variability of two random variables. 86
- CPG Central Pattern Generator: A neural circuit that produces rhythmic outputs in the absence of rhythmic input. 3, 11, 49, 50, 51, 54, 56, 57, 58, 59, 61, 62, 64, 67, 68, 70, 72, 101, 106, 110, 114, 120, 124
- CX Central Complex: A central neuropil that is located in the medial protocerebrum of insect brains, associated with self-location within the environment. 29, 31, 42, 43, 44, 45, 79, 97, 124
- **Flip-Flop** A periodic switching of the strength of spiking activity between two halves. 49, 50, 54, 58, 67, 68, 69, 120, 124
- **FoV** Field of View: The angular amount of the entire visual scene covered by a visual sensor. 80, 82, 84, 86, 88, 89, 91, 92, 94, 103, 104, 108, 113, 121, 122
- LAL Lateral Accessory Lobe: Paired neuropils that are located in the medial protocerebrum of insect brains, associated with pre-motor control. 3, 4, 6, 10, 11, 12, 13, 22, 26, 27, 28, 29, 31, 48, 49, 50, 51, 52, 79, 80, 86, 92, 95, 97, 101, 102, 117, 118, 119, 121, 123, 124, 125
- MB Mushroom Body: Paired neuropils that are located in the medial protocerebrum of insect brains, associated with memory formation. 29, 31, 79, 80, 97, 98, 121, 123
- **Neck connective** The structure resembling a neck in insects, connecting the head with the thorax. 28

- **Neuropil** A dense network of interwoven nerve fibres as well as their branches and synapses. 29, 31, 42
- Offset Generating memories for snapshot navigation with body orientations not aligned with the desired orientation. 75, 80, 83, 84, 85, 88, 89, 94, 95, 97, 103, 112, 113, 121, 122
- **PI** Path Integration: Calculating one's current position in relation to a starting position by using estimates of speed and direction. 41, 46, 97
- **rIFF** rotary Image Familiarity Function: A strategy to recover the most familiar view direction in a position compared to a memorized view. 82, 86, 103, 104, 106, 107, 108, 110, 113, 114
- Snapshot Navigation Recovering movement direction by aligning a current view with a memorized view. 4, 77, 78, 81, 92, 94, 97, 98, 102, 104, 108, 109, 112
- **SNN** Spiking Neural Network: A computational model of neuronal currents represents each neuron. When the current of a neuron surpasses a threshold, it spikes, thereby exciting or inhibiting other neurons it is targeting. 3, 4, 10, 11, 13, 53, 54, 56, 61, 99, 104, 105, 106, 107, 110, 111, 112, 114, 118, 123, 124
- **Zig-Zagging** The periodic direction change between leftward and rightward rotation. 3, 10, 47, 48, 62, 63, 64, 65, 66, 67, 68, 69, 72, 74, 101, 105, 113, 114, 119, 120, 122, 125

Abstract

Insects have developed small scale search behaviours to pursue navigation relevant stimuli more effectively. These often resemble a variation of Zig-Zagging, steering periodically to the left and right, therefore increasing the sampling. In this context we investigate the role of a homologous insect brain structure, the Lateral Accessory Lobe (LAL), which has been described as a pre-motor centre but received limited attention so far.

Following a synthesis of the literature on the LAL we developed a steering framework, which proposes that with lateralised stimuli as input, the LAL can initiate a Zig-Zagging behaviour if the input is too weak, meaning unreliable, and targeted steering behaviours if the input is strong, thus reliable.

Based on this framework we model a Spiking Neural Network (SNN) investigating a sensory modulated Central Pattern Generator (CPG) as a possible neural mechanism enabling adaptive search behaviours. We investigated the parameter space of the model to discover both the range of possible behaviours as well as which parameter combinations lead to the previously described behaviour. We found that no parameter combination accounts for the majority of observed behaviours. Furthermore, changing the computational noise levels does not lead to break-down of this behaviour. We conclude, that this neural architecture is robust to generate an adaptable Zig-Zaggingg behaviour. Additionally, we developed a more comprehensive network to explore the functions of known neuron-types with regard to motor control.

To investigate how this steering framework might work for view based navigation, we investigated how lateralised sensory input can be used for snapshot navigation. We used a 3D-reconstruction from a LiDAR-scanned field-site ("Antworld") to generate

realistic visual stimuli. Instead of using the entire panorama, we subdivided this into two Fields of View for snapshot generation and the later image comparisons. The difference of image familiarity from both sides was subtracted to initiate a steering response into the most familiar direction. We found that a bigger Field of View alongside non-forward facing memories generated the most correct steering responses towards the snapshot direction. This demonstrates that the LAL-inspired steering framework can be functional for a complex sensori-motor task that had previously not been implicated in LAL functionality.

Finally, we modelled how bilateral sensory information and a SNN model of the LAL behave in a snapshot navigation setup using Antworld. We compared the original snapshot navigation model using a panoramic Field of View with several combinations of the Core-Network and bilateral vision models: using a bilateral view, a bilateral view with the SNN, a panoramic view with SNN and other standard movement behaviours. We confirmed the findings of preliminary work, in an abstract setup, that had shown that a bilateral view combined with a SNN performs best to recover and approach navigation relevant locations. Also introducing models based on the steering framework into this visually complex environment improved the performance of agents performing snapshot navigation.Snapshot Navigation

Acknowledgements

I (FS) dedicate this thesis to my family, who supported my whole academic journey. It all began with my grandmother teaching me about animals, how they looked like, their behaviours and their names. This fuelled my everlasting curiosity of how things work, especially animals of all kinds. Over teenager years, another passion of mine formed - science fiction. SciFi taught me to dream about making creations of ones imagination and then to work out how to do that. Over the years, my mother taught me to dedicate myself to something and by persevering through tough challenges, the resulting outcome would be desirable. Thank you for everything mum, you are the best!

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1 Research contributions

The overall context of this project was to explore the biomimetic pipeline from insect neural circuits to plausible controllers for navigating agents. Across four research Chapters, I have presented connected blocks of work, that lead from the knowledge base of insect neuroscience through to explorations of sensory systems and SNN controllers that could play a role in visual navigation. Here, I summarise the contributions from each of the research chapters.

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

Insects have evolved small scale search behaviours to pursue navigation relevant stimuli more effectively. These often resemble a variation of Zig-Zagging, steering periodically to the left and right, therefore increasing the rate of sensory sampling. In this context we investigate the role of a homologous insect brain structure, the Lateral Accessory Lobe, which has been described as a pre-motor centre but received limited attention so far. From a synthesis of the available literature we proposed a steering framework, which suggests that targeted steering and active small scale search, across many insect species and sensory modalities, can be driven by the conserved neural circuits in the insect LAL. Lateralised sensory inputs can initiate a Zig-Zagging search-like behaviour if the input is too weak, meaning it is unreliable. Conversely targeted steering behaviours will be produced if the input is strong, thus reliable.

Achievements

- A comprehensive review of the known neurophysiology of the Lateral Accessory Lobe across insects and a variety of sensory-driven behaviours.
- 2. A novel steering framework that unifies multiple neural features and behavioural observations. The framework captures the adaptive functional qualities of the

LAL and provides the starting point for a biomimetic investigation of its usefulness for autonomous agent control.

 Steinbeck, F., Adden, A., and Graham, P. (2020). Connecting brain to behaviour: A role for general purpose steering circuits in insect orientation? Journal of Experimental Biology, 223.

1.2 Production of adaptive movement patterns via an insect inspired Spiking Neural Network Central Pattern Generator

Based on the steering framework, we developed two Spiking Neural Network models investigating how biologically plausible sensory modulated Central Pattern Generators (CPG) could be a possible neural substrate to enable adaptive search behaviours. We put forward a comprehensive network to explore the functions of the known neuron-types with regard to motor control and distilled this network to establish the core functional components. Through an investigation of the parameter space of the core model we found that no narrow range of parameter combination accounts for the majority of observed successful networks that produce the desired adaptive behaviours neither does increased noise inhibit the output behaviour. This suggests that the network architecture itself is a robust driver of the adaptive active search behaviour.

Achievements

- A comprehensive SNN model which integrates extensive knowledge of neuron types within the LAL. This is the most up-to-date model of the LAL and the first model both to use spiking neurons and suggest how a CPG can be formed by the inherent LAL circuitry.
- 2. A "core" SNN that distils the adaptive functional properties of the LAL and provides the basis for potential biomimetic autonomous agent controllers.

 Production of adaptive movement patterns via an insect inspired Spiking Neural Network Central Pattern Generator. (2022) Fabian Steinbeck, Thomas Nowotny, Andrew Philippides and Paul Graham, Frontiers in Computational Neuroscience, submitted.

1.3 A bilateral vision approach to view-based navigation

A key component of our steering framework comes from the fact that insect sensory systems appear to be bilaterally organised. Our ultimate target behaviour was view-based navigation, where the predominant algorithms use a single "cyclops" like visual input. Therefore, we investigated how lateralised sensory input can be used for snapshot navigation. We used a 3D-reconstruction from a LiDAR-scanned field-site ("Antworld") to generate realistic visual stimuli. Instead of using the entire panorama, we subdivided this into two Fields of View for snapshot generation and later image comparisons. We demonstrated that a simple Left-Right comparison between familiarity values for current versus stored views, was an ideal steering signal when memorised views were Offset to the route direction. Further, we found that a larger Field of View and broad range of Offsets robustly generated correct steering.

Achievements

- 1. A systematic investigation and existence proof of how a bilateral organisation of views can be successful for familiarity based visual navigation.
- 2. The first investigation of how visual familiarity might interact with the insect premotor areas (LAL) during view based navigation.

1.4 A bio-inspired snapshot algorithm using active sensing

Finally, we modelled how active sensing and bilateral sensory information behave together during a snapshot navigation scenario mimicking the navigation challenge of desert ants. We compared a snapshot navigation model using a panoramic Field of View with several combinations of the models we have developed: a bilateral view, a bilateral view with a SNN driving active search, a panoramic view with SNN and other standard movement behaviours. We confirmed our previous results from an abstract model, where a bilateral view combined with a SNN performs best to recover and approach goal locations. More generally we can say that introducing models based on our steering framework improves the performance of view based navigating agents in a complex simulation of a real environment.

Achievements

- We give the first example of a SNN pre-motor model driving active sensing during view-based homing. Thus we give existence proof of the viability of LAL circuits in visual navigation - a more complex sensori-motor behaviour than those previously implicated in LAL outputs.
- 2. We demonstrate that both bilateral sensory inputs and active search behaviours can improve navigation performance, thus highlighting useful features of insect navigation for potential biomimetic application.
- Steinbeck, F., Graham, P., Nowotny, T., and Philippides, A. (2020b). Can small scale search behaviours enhance large-scale navigation? In P. F. M. J. Vouloutsi, Vasiliki and Mura, Anna and Tauber, Falk and Speck, Thomas and Prescott, Tony J. and Verschure (Ed.), Biomimetic and Biohybrid Systems (pp. 338—-341). Springer International Publishing, biomimetic edition.

2 Chapter 1: The bio-mimetic potential of insect visual navigation circuits

2.1 Introduction

Insects are capable of navigating long distances through complex environments. Irrespective of brain size, many species have advanced navigational abilities enabling the exploration of their environment and exploitation of dispersed resources within it. The research of the mechanisms underlying these abilities has gained momentum over the last decades or so. While this can be partially attributed to the genetic tools available to study neural circuits in *Drosophila*, animal behaviour studies and engineering disciplines have also contributed to our understanding. Biomimetic engineers are especially attracted to insect navigators, for the following main reasons.

Insects have generally quite poor sensory apparatus quality compared to other species' sensory systems, for example the eyes of visually navigating ants possess a resolution of 1°-4° (Schwarz et al., 2011). While this may seem as a downside, this potential limitation does not affect their navigation abilities in a significant way. Furthermore, insect brains are tiny (ants have less than \sim 500,000 neurons in their brain, Godfrey et al. (2021)). Yet, they can achieve quite complex behaviours. Some migrating insect species like the monarch butterfly can transverse thousands of kilometres without getting lost (Heinze et al., 2013), whereas pinpoint accuracy is achieved by bees, which go out foraging and then return to their nests, often covering distances of up to 6 kilometres (Waddington et al., 1994). Close inspection of the insect circuits underpinning navigation show that there are a few neuronal bottlenecks, at which only a few neurons process the inputs from a much higher number of sensory neurons, thus suggesting highly efficient computational principles (Dewar et al., 2017). No human engineered system has yet come close to navigating with insect like performance in a truly autonomous fashion, that is with only on-board processing and without an external positioning information. Many solutions still heavily rely on offboard computation power, while the onboard equipment also often is very "expensive" (energetically and money-wise). Areas of progress, such as with SLAM (Simultaneous Localisation And Mapping, Smith & Cheeseman (1986)) are heavily reliant on object recognition and 3D-reconstruction, which make these approaches data-heavy and computationally expensive. Thus overall, it is clear that there is engineering potential to be taken from insects who may shine a light on how computationally efficient algorithms can drive robust high performance navigation.

Here, we review visually related sensory systems, neuronal structures and computational principles, that serve the visual control and navigation behaviours of insects. We showcase why the circuit characteristics are ideal candidates for biomimetic algorithms that may solve engineering challenges.

2.2 The insect brain

The basic ground plan of the insect is a conserved brain structure that is seen across arthropods. Indeed this basic ground-plan is even argued to be homologous to that of vertebrates (Strausfeld & Hirth, 2013). Distinct neuropils in the insect brain are easy to observe and describe across species and this modularity has enabled progress to be made regarding the structure-function relationships. There are still brain area functions which are yet to be determined. However, we have been able to identify the key brain areas for tasks that are behaviourally explicit and easy to describe. Here, we concentrate on brain areas which functions are mapped out well within the task of visual navigation (Webb & Wystrach, 2016). Figure 1 shows the basic brain organisation for a typical insect, highlighting the sensory input anatomy and the major



integrative brain centres.

Figure 2.1: The basic insect brain organisation highlighting navigation relevant areas. The optic lobes [yellow] are large bilateral structures which process retinotopically organised visual information through an anatomically distinct series of layers. Olfactory lobes are the other main input area. The brain has two major integration centres. The bilaterally organised Mushroom Bodies [red] are the major associative learning centres for olfactory and visual information. The central complex [light green], takes information from many other brain regions and is responsible for maintenance and organisation of orientation information and generating pre-motor signals.

2.3 Peripheral visual sensors

The compound eye is different to the simple eyes of humans. Instead of focussing light onto a sheet of photoreceptors, compound eyes are built up from many simple eyes, where each simple eye effectively produces one pixel. The individual visual units are called ommatidia and each has it's own lens and photoreceptors.

Compound eye inspired imaging devices offer advantages over traditional camera systems. Primarily through the ability to engineer an arbitrary field of view with less bulky hardware, but also the insect-like ability to match optical hardware to specific tasks (Yang et al., 2018). For instance, Cogal et al. (2014) present a large FOV system for endoscopy tasks, where interestingly the inherent flexibility of the optical array allows spaces for lighting. However, many uses are in applications that more closely resemble the sensory ecology of insects. Maddern & Wyeth (2008) take a more insect like inspiration, looking at self-motion detection at high speed (600 fps) with very low power consumption (100mW), similar approaches have also been applied to robots, again where power consumption and rapid imaging are important (Expert & Ruffier, 2015; Briod et al., 2016).

As with all animals, different insect species have ecologically tuned colour vision for certain tasks, with achromatic vision being mediated by green photoreceptors (Briscoe & Chittka, 2001). In navigating insects such as ants a prominent source of information comes from the high contrast boundaries between terrestrial objects and the sky (Graham & Cheng, 2009). The extraction of this contrast boundary is facilitated by the spectral tuning of the prominent photoreceptor types, which are tuned to Ultraviolet and Green light (Möller, 2002; Kollmeier et al., 2007) and when used as part of an opponent process will extract skyline information that is robust to variations in lighting. The use of UV contrast as a robust way to extract skyline information for localisation via panoramic visual memory has been shown in urban environments by Stone et al. (2014).

The pioneering studies of Rüdiger Wehner (1984) on the navigation of desert ants demonstrated that insects are able to use celestial visual information to derive compass information. One of the dominant celestial cues comes from polarisation patterns as skylight is polarised due to scattering in the atmosphere. The dominant linear axis of polarisation systematically varies across the sky and insects are able to compute absolute compass information from this pattern (Gkanias et al., 2019). The visual input to compass systems comes from specialised ommatidia in the dorsal region

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of the eye (Labhart, 1980) that are sensitive to polarised light, an example of how compound eyes often have heterogeneous function in different regions of the visual field. Compass sensors inspired by insects have been developed for robotic orient-ation (Lambrinos et al., 1997; Dupeyroux et al., 2019b) and have shown impressive accuracy and robustness (Serres & Viollet, 2018).

While the complex eyes are thought to produce form-vision capable of perceiving objects, there are other visual organs. The Ocelli are invertebrate simple eyes, of which there are usually three, and they sit on top of the head. These are thought to have excellent light detection abilities and may play a role in maintaining flight stability. Ocelli are not image forming, as the photoreceptors are not in the focal plane of the lenses. However, their function as wide-field luminance sensors means they respond to the kind of large visual changes that happen due to self-motion, such as pitch or roll in flying insects (Gremillion et al., 2014). Parsons et al. (2010) showed that in flies the ocelli have faster connections to the muscles involved in flight stabilisation than the compound eyes and that function for flight stabilisation has been captured in simple, fast analogue hardware (Fuller et al., 2014).

2.4 Visual computation in the optic lobes

In the optic lobes (Figure 2.1) visual stimuli get processed in a series of layers. Initially by the Lamina, Medulla, then Lobula and in some species with an additional Lobula Plate. The early layers are responsible local visual calculations, such as contrast enhancement, normalisation and motion detection. The later layers (Lobula and Lobula Plate) contain small numbers of wide-field neurons that act as matched filters for patterns of optic flow and figure-ground discrimination.

The local computations, such as movement detection can be incorporated into bio-

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inspired designs for speed detectors and obstacle avoidance. This is shown in an early example of insect inspired biorobotics (Franceschini et al., 1992). Where simple motion detection between two photoreceptors of a neuromorphic eye could be tuned to detect objects at a fixed distance. Similarly, speed estimates can be derived from similar circuits (Franceschini et al., 2007). These local computations are similar to the processing undertaken in artificial compound eye systems (see above). However, at the next layers of the insect optic lobe we see more complex visual integration that provides more complex or robust visual information for orientation.

2.4.1 Visual behaviours using wide-field visual information

The wide field pattern of visual motion, optic flow (OF), provides information about both an agent's movement and thus the the structure of the environment. Furthermore, this information is defined by simple geometry and Thus the wide-field optic flow tuned neurons in the later layers of the optic lobe can be hardcoded as direct matched-filters for behaviourally relevant information.

A very important behaviour for most animals is a predatory escape response. A thoroughly studied example is the Lobular Giant Movement detector in the locust (O'Shea & Williams, 1974). This neuron covers the whole visual field of each compound eye. When a stimulus expands within the field the neuron becomes active. This activity is integrated over time until a threshold is reached and the escape response is initiated. This mechanism stays consistent even with background luminosity and contrast (Gabbiani et al., 1999).

This mechanism has been applied in both a robotic application and for the detection of collision danger for cars. Applied in a robotic setup, a integrate-and-fire version of the LGMD model generated a reliable collision avoidance response over a whole range of velocities (Blanchard et al., 2000). Dedicated for a method of collision avoidance in cars, and in combination with the usage of elementary motion detectors, a robust collision avoidance response could be produced for a wide range of possible traffic situations using real world images(Stafford et al., 2007).

Another insect behaviour that relies on OF information is the compensatory behaviour in flying insects, which aims to keep the amount of optic flow the same coming from both eyes. If the amounts are manipulated, the insect can be made to fly down a corridor very close to one wall instead of the middle, which they usually would do (Serres et al., 2008). Landing in bumblebees also has been shown to depend on optic flow. While descending, the amount of OF is kept constant, leading to a deceleration proportional to the height (Srinivasan et al., 2000). These control algorithms derived from bees have provided inspiration for a long career of bio-engineering from Mandyam Srinivasan (2021) and more generally, there are examples of robots using wide-field OF for flight control (Humbert & Hyslop, 2012; Cope et al., 2016). Without the use of GPS or radar, with onboard-computations only, OF can be used to determine the direction of flight, the height, the distance travelled and be used for safe landings.

2.5 The Central Complex

The insect Central Complex is a conserved brain structure seen across all arthropods that is made up of central and paired structures generally involved in the organisation of multi-modal orientation relevant information and the generation of motor commands (Turner-Evans & Jayaraman, 2016). The major regions are the Fan-Shaped Body, Ellipsoid Body and the Protocerebral Bridge. In terms of navigation, the circuit formed by the ellipsoid body and the Protocerebral Bridge is key for keeping track of current heading and the output region is crucial for steering and driving active sampling (see below). However, computational models of the Central Complex have highlighted more general properties of insect-inspired circuits that might be advantageous for autonomous agents in future. For example: Fiore et al. (2017) and Sun et al. (2020) demonstrate how the Central Complex is well suited to the processing of multimodal input signals, potentially extending to novel, non-biological, sensors; And, Cope et al. (2017) show how the Ellipsoid Body circuitry can use plastic connections to maintain accurate representations of local visual orientation information. Whilst these models are currently aimed at testing biological ideas, it is exciting that computational neuroscience might soon provide plausible circuits that could be part of adaptive controllers for robots.

2.5.1 Compass information and path integration

As described above insects are have the capability to detect polarized light. This directional information is integrated with other sensory cues that indicate geocentric directions in the Protocerebral Bridge of the CX. Neurons from discrete columns in the PCB respond to specific orientations of polarisation (Pfeiffer & Homberg, 2014) and this information is connected to the Ellipsoid Body to form a ring attractor circuit that keeps track of orientation. Many insects can integrate this direction racking system with information about movement speed to generate and maintain a homing vector. This mechanism allows them to explore environments while always remembering where they started their journey from. So called Path Integration (Müller & Wehner, 1988) is an important method as it allows a mobile agent to explore novel terrain and safely return to the origin. Thus it is a mechanism that can scaffold the learning of information by providing guidance during early exploration. While this type of navigation is widespread in animals and has been used for centuries in naval navigation by sailors, autonomous technologies using bio-inspired versions of this method are rare. A recently developed robot (the legged AntBot) by Dupeyroux et al. (2019a) shows promising outdoor capabilities. Using two UV-light sensors and a 12-pixel optic-flow sensor, they were able to successfully integrate the compass information with the distance information provided by stride and optic flow. Homing towards a place of origin, this real-world application reached the origin with an error of 0.7% only.

From a computational neuroscience perspective, Stone et al. (2017) provide a circuit model of the Central Complex which provides a mechanism for a distributed circuit that uses the 8-fold circular symmetry of the Central Complex to update a population of distance accumulators mapped to the directions of the Ellipsoid Body ring attractor circuit.

2.5.2 (Pre-)Motor control

The output region of the Central Complex, which converts orientation information to motor commands, is the Lateral Accessory Lobe (LAL). It receives connections from all navigation related brain structures and projects directly to the motor centres in the insect thorax (Namiki & Kanzaki, 2016; Steinbeck et al., 2020a). Although the area has not yet been extensively studied it is possible to propose how the known architecture relates to the adaptive properties.

The LAL, a pre-motor centre is involved in both the generation of targeted steering behaviours (Zorović et al., 2011) and small scale search behaviours (Kanzaki et al., 1992; Pansopha et al., 2014). An imbalance of neuron activity between both hemispheres results in steering (Iwano et al., 2010; Zorović & Hedwig, 2013), speed and turning may be controlled independently of each other by dedicated neurons for each (Bidaye et al., 2020; Rayshubskiy et al., 2020).

Most modelling attempts have concentrated on either the steering aspect (Fiore et al., 2015, 2017) or the generation of small-scale search behaviours (Mishima & Kanzaki, 1999; Adden et al., 2020). The most recent attempt explores both aspects in unison by exploring the individual functions of the LAL's neuron types and suggests a Cent-

ral Pattern Generator as biologically plausible mechanism producing the small scale search behaviours (see Chapter 4). This model then was applied in several navigation scenarios, producing biologically plausible navigation behaviours and improving the performance of snapshot navigation algorithms (see Chapter 6 and Appendix).

2.6 Associative learning in the Mushroom Bodies

The importance of the Mushroom Bodies for navigation in social insects is highlighted by the correlation between spatial behaviour and MB size (Farris, 2013), alongside MBs long being known to be important for olfactory associative learning and food memories (Heisenberg, 2003). The hypothesised role for MBs in visual navigation (Webb & Wystrach, 2016) has recently been demonstrated for two species of ants (Buehlmann et al., 2020; Kamhi et al., 2020) where lesions of parts of the MB lead to a deficit in visual navigation.

The architecture of the MB means that as well as providing a location for stored visual memories, it is also attractive as a general purpose learning machine. The input signals to the MB arrive at a large population of Kenyon Cells, such that the KC code is a sparse representation of the input. These KC cells connect to output neurons at dopaminergic synapses. Thus aversive or appetitive memories can be formed of the sensory inputs represented by the currently active pattern of KC cells (Webb & Wystrach, 2016). The potential for navigational view memories to be learnt with an MB architecture was shown by Ardin et al. (2016). In a simulated environment navigation was implemented by the MB outputting a signal that represented whether a particular scene had previously been reinforced (Baddeley et al., 2012).

Crucially, in contrast to Machine Learning methods that rely on deep neural networks, MB models can learn visual scenes rapidly and update memories online whilst

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moving through the environment. This highlights the distinction in learning style for bio-inspired methods and some ML approaches reliant on extensive training. These properties have encouraged some to look at the MBs as inspiration for general purpose learning architectures (Aso et al., 2014) with applications beyond navigation. Dasgupta et al. (2017) and Chancan et al. (2020) both show how aspects of the MB organisation of insects can be abstracted to provide robust rapid learning and generalisation across learned categories, given appropriate sensory organisation.

2.7 Summary

The insect brain offers a vast range of mechanisms inspire biomimetic engineers. This pipeline has been successful in capturing the performance and utility of the visual periphery using analogue hardware. Thus, there exist specialised and highly efficient sensor hardware that capture some of the functionality of insect vision for root control tasks, such as obstacle avoidance or flight control.

For navigation models derived from central brain areas such as the CX and MBs, the current state of the art are computational neuroscience models addressing cutting edge biological hypotheses. However, some of these models are already being tested on robotic platforms, therefore these models can soon become feasible alternative methods for reliable and robust navigation technologies. The development of neuromorphic technology and the impressive speed of GPU enhanced neural networks (Yavuz et al., 2016) now means that insect inspired network models are viable candidates for robot control (Dalgaty et al., 2018; Knight et al., 2020). This has led to research groups attempting to develop insect inspired robot control and navigation technologies, such as the Brains on Board project, so game changing systems can be expected in the very near future. In this spirit, we have investigated the pre-motor areas of the insect brain. Both to further biological understanding, but also to investigate the plausibility of biomimetic algorithms being developed that are based on our understanding of the structure-function relationships in this part of the insect brain.

3 Chapter 2: Connecting brain to behaviour: a role for general purpose steering circuits in insect orientation?

This chapter was written and the framework developed by FS. AA supported with expert knowledge of the neurobiological substrate. PG supported editing.

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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.

3.1 Introduction

The behavioural repertoire of insects includes a variety of sensory drive 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 & 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 (Wehner & Räber, 1979; Müller & Wehner, 1988) and bees (Von Frisch & Lindauer, 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; Stone et al., 2017; Kottler 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), 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 & 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), 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 & Kanzaki, 2016) and give rise to neurons that project through the Neck connective 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 wellstudied 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 sensorydriven 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 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.

3.2 LAL neuroanatomy is homologous across species

The LALs [or iDFP in *Drosophila* (Chiang et al., 2011) and ventral body in Diptera (Strausfeld & Li, 1999)] are paired Neuropils located in the medial protocerebrum of insects. They are located laterally to the central complex and are bordered by the 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 & Homberg, 2009; Heinze et al., 2013; Kanzaki et al., 1992; Strauss et al., 1992; Lin et al., 2013).

The LALs also receive a variety of other sensory inputs (figure 3.1B). These include inputs from a range of visual processing areas, such as the medulla, the lobula, the lobula plate (Namiki & Kanzaki, 2018) and the anterior optic tubercles (involved in the processing of polarised light; Heinze & Homberg (2008)). Olfactory inputs from the antennal lobes are transmitted to the LALs via the superior medial protocerebrum (Mishima & 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 & Laurent, 2007) and cognitive processing (Menzel & Giurfa, 2001) in complex orient-ation tasks, as demonstrated by their size correlating with the complexity of foraging

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tasks in social insect species (Bernstein & Bernstein, 1969; Farris & Schulmeister, 2011).



Figure 3.1: **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 Roessler Group in Wuerzburg). 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.

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, 2014; Namiki & 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, 2014) and the visual processing areas (Namiki et al., 2018; Namiki & Kanzaki, 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 (figure 3.2A,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



Figure 3.2: **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 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.

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, 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 presynaptic branches of innervating neurons do not seem to be separated into different regions for different sensory modalities of LAL input (Namiki, 2014).

3.3 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*; figure 3.3A). 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 byproduct 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 moths' path will depend on the amount of pheromone, with search strategies naturally structured by the history of pheromone absence (Namiki & Kanzaki, 2014; Pansopha et al., 2014).



Figure 3.3: **LAL-mediated behaviours in silkmoth and cricket.** (A) Pheromonetracking 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 zigzag 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.

Kanzaki and colleagues identified the LAL as being key to the generation of the observed zig-zag searching portion of the behaviour (Kanzaki et al., 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 et al., 1992; Kanzaki & Shibuya, 1992; Mishima & Kanzaki, 1999). The firing activities of the Type I neurons from the two hemispheres are in antiphase, 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 flip-flop neurons correlate strongly with motor output during pheromone-seeking behaviour (Iwano et al., 2010; Namiki & 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 et al. (2011); figure 3.3B). 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 (figure 3.2C). 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 & 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 figure

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3.2C). 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.

3.4 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 (figure 3.2) (Iwano et al., 2010; Namiki & Kanzaki, 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 et al., 2011; Zorović & Hedwig, 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.



Figure 3.4: **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. Type II neurons may coordinate the LAL-VPC interactions and Type III neurons the interhemispheric interactions within the LAL. 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.

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 (Pansopha et al., 2014). In crickets, LAL neurons that are

Figure 3.5: 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; \pm , 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.

sensitive to auditory cues are additionally sensitive to visual and mechanosensory stimuli (Zorović & Hedwig, 2013). In flies (Huston & Krapp, 2008; Schnell et al., 2017; Wertz et al., 2012), honeybees (Bidwell & Goodman, 1993; Goodman et al., 1987; Ibbotson et al., 2017) and locusts (Träger & 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 (Olberg, 1983; Wessnitzer & Webb, 2006; Wolff & Strausfeld, 2015). In order to optimally integrate turning signals, the inputs should also incorporate 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 (figure 3.4), such as stochastic turns or casting; secondly, we propose that when task-relevant stimuli are available, the LAL network acts to integrate the available information in order to generate directed turns (figure 3.5).

3.5 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 & 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 & 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 (figure 3.4).

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 PI and visual guidance (Collett, 2012; Hoin-ville & 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 (figure 3.5).

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; ljspeert, 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 & 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, 2016). 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 & 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 & Mishima, 1996) that control head direction, and that their activity precedes full-body turns in walking as well as flying insects (e.g. Land et al. (2013)); 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, asymmetrical muscular activity on each side of the body is required (Bidwell & Goodman, 1993; Goodman et al., 1987); 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 & Büschges, 1998; D'Avella et al., 2015; Schilling & Cruse, 2020).

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Thus, the descending control signals that need to alter the thoracic motor pattern from walking to turning (Hellekes et al., 2012; Mu & 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 & 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 (Harley & Ritzmann, 2010). 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 melanogaster* (Cande et al., 2018). 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 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 (figure 3.1B; Homberg (1994); Namiki et al. (2018, 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 pheromonetracking 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, 2018). Furthermore, other processing areas, such as the CX, also receive feedback from the LAL (Homberg, 1994; Heinze, 2015). Thus, it may be effective to generate efference copies of steering commands during LAL processing, and feed these back to other processing areas.

3.6 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 & 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, 2019). Similar motor patterns are also seen in PI-driven search (Wehner & 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.

4 Chapter 3: Production of adaptive movement patterns via an insect inspired Spiking Neural Network Central Pattern Generator.

This chapter was written and the experiments designed and executed by FS. PG and TN supported with the experimental designs and editing. This chapter has been submitted to Frontiers in Comp NS.

Abstract

Navigation in ever-changing environments requires effective navigation behaviours. Many insects have developed adaptive movement patterns which increase their success in achieving navigational goals. A conserved brain area in the insect brain, the Lateral Accessory Lobe, is involved in generating small scale search movements which increase the efficacy of sensory sampling. When the reliability of an essential navigational stimulus is low, searching movements are initiated whereas if the stimulus reliability is high, a targeted steering response is elicited. Thus the network mediates an adaptive switching between motor patterns. We developed Spiking Neural Network models to explore how an insect inspired architecture could generate adaptive movements in relation to changing sensory inputs. The models are able to generate a variety of adaptive movement patterns, the majority of which are of the Zig-Zagging kind, as seen in a variety of insects. Furthermore, these networks are robust to noise. Because a large spread of general network parameters lead to the correct movement dynamics, we conclude that the investigated network architecture is inherently well suited to generating adaptive movement patterns.

4.1 Introduction

A key component of the adaptive behaviour of natural and artificial systems is motor control. Adaptive behaviour often requires agents to produce active movement strategies to both acquire useful sensory information and then use it to their advantage. For instance, in visually guided behaviours in insects, we see many examples of movement strategies that can be described as active vision: ranging from saccadic flight structure in bees that helps extract visual depth information (Wagner, 1986), peering in locusts (Wallace, 1959) to whole body rotational scanning movements in navigating ants (Wystrach et al., 2016b). Some of these active vision behaviours seem to be a prevalent type of search behaviour, whereby individuals are seeking behaviourally relevant sensory information, i.e. Zig-Zagging while landing using vision in bees and wasps (Collett et al., 2016; Lehrer & Collett, 1994), sinuous ant trajectories when visually homing (Buehlmann et al., 2018) and can be shown to increase performance in simulated or robot navigation (Steinbeck et al., 2020a; Kodzhabashev & Mangan, 2015; Steinbeck et al., 2020b). Such active behaviours are also seen in insects "searching" for behaviourally relevant information from other modalities such as moths when searching for pheromones (Kanzaki & Mishima, 1996; Pansopha et al., 2014; Mishima & Kanzaki, 1999). One particular brain area, the Lateral Accessory Lobe (LAL), has been shown to be a key-component in the generation of search related motor signals controlling behaviours such as the pheromone search highlighted above (Kanzaki & Shibuya, 1992). The LAL is also referred to as a pre-motor area and is the gateway for signals from the higher processing brain areas on their way to motor centres (Namiki et al., 2014; Namiki & Kanzaki, 2016). In general, the LAL seems to transform navigation related sensory signals into turning signals, which then can be realised by the motor system downstream (Bidaye et al., 2020; Bidwell & Goodman, 1993; Rayshubskiy et al., 2020; Zorović & Hedwig, 2013), however it can also generate intrinsic motor patterns in the absence of sensory information.

If the incoming sensory signals to the LAL are strong and reliable, these are directly passed on to the motor system for targeted steering. This has been demonstrated in crickets, who steer towards the calls of conspecifics (phonotaxis), with the LAL in-

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volved in initiating the steering movements (Zorović & Hedwig, 2013). However, if the incoming signals are weak and unreliable, the LAL seems to be capable of generating a rhythmic signal, which results in alternating turning directions which actively increases the sampling of the sensory world. This is seen for instance in the upregulation of scanning in ants that experience visual uncertainty (Wystrach et al., 2014), but the most prominent example is the zig-zag walking behaviour in silkmoths, which is initiated when losing the pheromone plume. As with targeted steering, the neural origin of these 'search' behaviours has also been shown to be the LAL (Kanzaki & Shibuya, 1992). The left and right lobes of the LAL appear to phasically inhibit contralateral output neurons ("Flip-Flopping", Iwano et al. (2010)), and the turning itself seems to be initiated by a difference of firing rate between the left and right descending pathways (Rayshubskiy et al., 2020; Zorović & Hedwig, 2013).

CPGs have been shown to be useful components for motor systems in bio-inspired robots that mimic well-studied motor circuits such as the walking CPGs of the stick insect (Mantziaris et al., 2020) or salamander (Ijspeert, 2008). CPGs are neural circuits that produce rhythmic outputs in the absence of rhythmic input. Possibly the simplest CPG to imagine is the so-called half-centre oscillator with two inhibitory, adapting neurons. If one neuron is firing faster, it will inhibit the other neuron. During that time, it would adapt to the longer stimulation and the firing rate would decline. This decline then would let the other neuron get stronger in turn, leading to an even faster decline of the firing rate of the first neuron. This back and forth leads to a phasically changing output between the two neurons. Thus, this CPG characteristics rely on the intrinsic properties of the neurons.

Computational models of the LAL have been developed to obtain a better understanding of how the LAL network's "Flip-Flop" activity might be generated. One of the first attempts used genetic algorithms to generate a model that produces a Flip-

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Flop activity and has approximately the same connectivity as observed in experiments (Chiba et al., 2010) . A recently developed rate-based model (Adden et al., 2020) was based on a suggested LAL-network connectivity from the silkmoth (Mishima & Kanzaki, 1999). The switch mechanism was hardcoded and inspired by neurons switching between low- and high-firing states. In simulations, the model reproduced aspects of silkmoth behaviour as shown by (Ando et al., 2013), where mounted Silkmoths on a robot followed pheromone plume edges. None of these models used a biologically plausible mechanism to reproduce the Flip-Flop activity.

LAL functionality is also invoked in larger models of the Central Complex of the insect brain, which is a brain area involved in control or orientation and heading (Pfeiffer & Homberg, 2014). The central complex is involved in path integration (PI) and recent models of PI use a simplified representation of the LAL, which consists of a left & right turning neuron (Stone et al., 2017; Sun et al., 2020) to integrate outputs of the PI network. Other models of a Central Complex brain area called the ellipsoid body, model exploring motor control learning provides a detailed account of the pre-motor role of the LAL by simply assigning the individual neurons of the LAL to different actions like forward and, left and right turning commands (Fiore et al., 2017). Furthermore, a mechanistically similar model showed how using a CPG may explain continuous lateral oscillations as a core mechanism for taxis in *Drosphila* larvae (Wystrach et al., 2016b). Thus across a range of models the functionality of the LAL and its connection to behaviour has been explored. Here, we build on these models to produce a biologically plausible model, that captures the general behavioural utility of the LAL pre-motor circuit.

Another related modelling approach used the reliability of a visual place recognition algorithm to modulate a sinusoidal trajectory with a robot, which would imitate antlike scanning behaviours algorithmically, but not the brain circuitry (Kodzhabashev & Mangan, 2015). We have recently developed a general steering framework (see figure 4.1, Steinbeck et al. (2020a)), in which we showed how the conserved circuitry of the LAL and its connections is an excellent candidate for producing both targeted steering and oscillating search behaviours across a wide ranges of insect behaviours utilising multiple sensory modalities. Based on this framework we present spiking neural network models inspired by the LAL; a Comprehensive model is constructed to explore the implications of diverse neurophysiological and neuroanatomical findings regarding the LAL region and its descending neurons. We further distil a Core network network which focuses on a network to produce the fundamental principles of the steering framework. The exact network connectivity within the LAL is currently unknown. Therefore, we based our models' connectivity on both the known global anatomy and our hypothesis how the observed output and correlated behaviours arise in the LAL. We explore how lateralized sensory input and lateralized motor circuits can integrate with a sensory modulated CPG to generate: (1) targeted steering for approaching a goal in response to the presence of sensory information; and (2) the generation of rhythmic output that can drive small scale searching patterns in the absence of reliable sensory information. Our aim is to demonstrate that the models can drive both these distinct behavioural modes, solely from the interaction of sensory input with intrinsic network dynamics.

We explore the properties of our networks by situating them in a simple simulated animat. The Comprehensive model demonstrates that the adaptive output can be created from a network with specific neuron roles that are hypothesised to be close to their biological functions (Bidaye et al., 2020; Rayshubskiy et al., 2020; Namiki et al., 2018; Schnell et al., 2017; Goodman et al., 1987; Ibbotson, 1991; Bidwell & Goodman, 1993). In the Core network we explore a wide range of parameter combinations and show how this network can robustly generate an adaptive range of movement

behaviours.



Figure 4.1: A general purpose steering framework based on the LAL. The two LAL compartments receive inputs from many sensory modalities from the ipsilateral hemisphere, both low level sensory information (like optic flow, haptic or olfactory signals) and highly processed information (path integration, place recognition). These inputs are differently weighted (w) and contain approach/aversion commands (\pm). If the receiving information is reliable (filled brackets), the turning signal will be directly gated through to the motor centres (C). B) If it is not reliable (empty brackets), a central pattern generator phasically flips the activity of the left and right output neurons. This leads to a search motif (D) and therefore to a higher sampling of the environment. While contralaterally descending neurons (Type I, orange) are mostly involved in steering, ipsilaterally descending neurons (Type II, green) and contralaterally inhibitory neurons (Type III, blue) are involved in the switching. LAL: Lateral Accessory Lobe, VPC: Ventral Protocerebrum. Schematic based on Steinbeck et. al 2020.

4.2 Setting up the simulations and parameter exploration

4.2.1 Implementation

The modelling and analysis were performed with MatLab 2017 & 2019 (The Math-Works, Inc., Natick, Massachusetts, USA).

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4.2.2 Central Pattern Generator model

The model is a spiking neural network (SNN), consisting of Integrate-and-fire neurons with adaptation ¹.

$$\frac{dV}{dt} = \frac{1}{C_m} (g_{\text{leak}}(V_{\text{leak}} - V) + g_{\text{adapt}} A^P (V_{\text{adapt}} - V) + I_0 + I_{syn})(1+\eta))$$
(1)

where the membrane capacitance $C_m = 0.5 \cdot 10^{-9}$ F, leak conductance $g_{\text{leak}} = 5 \cdot 10^{-9}$ S and leak reversal potential $V_{\text{leak}} = -60$ mV. Once the voltage surpasses a threshold $V_{\text{th}} = -50$ mV, a spike is emitted, the membrane potential clamped to $V_{\text{spike}} = 20$ mV for the next timestep, then to $V_{\text{reset}} = -65$ mV. The adaptation current is activated by spikes $A(t + \Delta t) = A + \Delta A$ (see tables 1,3 for values Δ A) and decays exponentially,

$$\frac{dA}{dt} = -\frac{A}{\tau_{\text{adapt}}} \tag{2}$$

and the conductance g_{adapt} , time scale adapt τ_{adapt} , exponent p (see tables 1, 3), and reversal potential $V_{adapt} = -70mV$. The term $1 + \eta$ implements multiplicative noise, where $\eta \sim u([0, 0.0086963])$, i.e. is a uniformly distributed random variable on the interval [x, y]². I_0 is a constant current offset that sets the spontaneous activity levels of the neurons (see tables 2, 4). The synaptic current I_{syn} is modelled with conductance based synapses,

$$I_{\rm syn} = g_{\rm syn} S(V_{\rm rev} - V) \tag{3}$$

where $g_{\rm syn}$ is the maximal synaptic conductance and the reversal $V_{\rm rev} = 0 {\rm mV}$ for

¹We chose a SNN format, because 1. This model should be ultimately applied on a robotic platform using SNNs, therefore we would not have to redo the work coming from a rate based model. 2. Similar insect brain models are developed as SNNs, too, which would make our model more compatible, if merged. 3. Finding intricacies leading to a certain behaviour may be easier to identify with more detailed SNN models than rate based models.

²The multiplicative noise was applied, being unaware initially that noise is traditionally added independently of the voltage change. As this whole parameter exploration was redone with independent noise, the multiplicative noise results were completely removed for the publication in Frontiers. Interestingly, the resulting trajectories using multiplicative noise looked smoother than using the independent noise

excitatory and $V_{\text{rev}} = -80$ mV for inhibitory synapses. The activation variable is incremented S(t + t) = S(t) + 0.1 for every presynaptic spike and decays according to

$$\frac{dS}{dt} = -\frac{S}{\tau_{\rm syn}} \tag{4}$$

with timescale $\tau_{syn_ex} = 20ms$ and $\tau_{syn_in} = 30ms$. The model was integrated with a forward Euler algorithm with constant time step t = 1ms.

The overall level of input to the networks is coding for the reliability of a not further specified sensory signal and enters into the input neurons E through static input currents in the range (0, $1.75 \cdot 10^{-9}$ V). High overall input current means a highly reliable signal and vice versa, similar as in basis function network modelling (Deneve et al., 2001). The balance of input on the left and right carries information about whether to go left or right, regardless of the overall signal strength. The networks here are designed so that the left hemisphere controls left turns and the right hemisphere controls right turns, as information has been shown to be processed unilaterally (Paulk et al., 2015), similarly to a Braitenberg vehicle (Braitenberg, 1984). Therefore, when receiving unilateral input, the SNNs are intended to generate a proportional unilateral output.

When the inputs are bilateral, the circuits should generate a Flip-Flopping output. Furthermore, weak sensory input should result in slow Flip-Flopping (leading to large exploratory turns), whereas strong activation of the CPG results in faster Flip-Flopping (leading to straight movements with small undulation). The outputs can then be used to directly generate movement (see Figure 4.2c).

The Comprehensive network explores the functions of more neurophysiological and neuroanatomical data. The two aspects explored here are: (1) the motor control is



Figure 4.2: **The LAL-inspired SNNs.** A - C: Comprehensive network. A) Top: Motor control split into velocity and turning. L = left turn, R = right turn, F = forward. Bottom: This network explores connectivity and neuron functions as described in the text with dedicated velocity and rotation neurons, leading to Ackerman steering. Neuron Abrevations: E = Excitatory Input, V = Velocity, IL = Ipsilateral Turning, CL = Contralateral Turning, A = Adaptation, I = Inhibition. B) Network activity plotted as Spike Density Functions (SDFs). C) Visual representation of the animat (not the actual actuator dimensions), and the trajectory generated with the activity depicted in B). D - F: Each letter shows the same as in A - C, but for the Core network. Both the CPG circuit neurons and descending neurons have been unified. Neuron Abrevations: E = Excitatory Input, I = adaptory Inhibition, O = Output, F = Force Integrators.

Colours for neurons: Grey = input, Orange = Velocity/ Output, Yellow = Ipsilateral turning, Red = Contralateral turning, Cyan = Adaptation, Blue = Inhibition/Adaptory Inhibition, Purple = Velocity Actuator. Brighter colours = Left hemisphere, darker colours = Right hemisphere.

split into velocity ("V"-neurons) and rotation neurons ("IL"-neurons and "CL"-neurons, Figure 4.2a), and (2) the CPG created by adapting ("A"-neurons) and inhibitory neurons ("I"-neurons, Figure 4.2a). Unilaterally descending velocity neurons (V) are connecting to both motor centre sides for velocity control and connect to the ipsilateral adaptory neurons (A). The adaptory neurons connect to the ipsilateral inhibitory neurons (I), which in turn connect to the contralateral velocity (V) and rotation neurons (IL, CL). This leads to a CPG with a few extra steps (see supplementary figure 4.8). Unilaterally descending rotation neurons (IL) connect to the ipsilateral motor centre initiating ipsilateral turns. Contralaterally descending rotation neurons (CL) connect to the contralateral motor centre initiating ipsilateral turns. They furthermore connect to contralateral ipsilateral rotation neurons (IL). In effect, this leads to a lesser turning command of the outside actuators than the inside actuators, as the outside turning radius is lesser than the inside turning radius, similarly to Ackermann steering.

The base layout of the Core network builds on the Comprehensive network in most aspects, but combines and simplifies the CPG circuit and the motor control (see Figure 4.2d). The computational algorithm is the same. Here, input neurons ("E"-neurons) make ipsilateral, excitatory connections to the CPG neurons ("I"-neurons) and output neurons ("O"-neurons). Each of the two CPG neurons provides inhibitory input to the contralateral CPG neuron and output neuron. The excitatory output neurons, which have been modelled to produce a spontaneous spiking rate of circa 30 Hz (as Type I neurons do (Iwano et al., 2010; Namiki & Kanzaki, 2016; Zorović & Hedwig, 2013), we took a mean of reported rates), and connect to the contralateral force integrators.

4.2.3 Embodiment

The actuators are modelled as non-spiking integrators. The maximum value they can achieve with prolonged excitation (spike trains) represents the maximum velocity each actuator can generate. Non-spiking integrators approximate the modelling of muscles (Wexler et al., 1997).

The actuator dimensions and movement values used are inspired by movements of *Melophorus bagoti* (Wystrach et al., 2014) and set into a Braitenberg vehicle (Figure 4.2c, f). Each actuator generates forward velocity independently. In the Core network, if the right actuator generates a higher velocity, the agent will turn left by rotating around the body centre point, and vice versa.

In the Comprehensive network, the forward motion and rotation are calculated independently from each other (figure 4.2a, top); both actuator sides generate leftward and rightward turning values, which are averaged for each actuator side first, then averaged over both actuators. The forward motion is the same for both actuators. As described in the previous section, due to the connectivity, this will produce Ackermann steering.

4.2.4 Parameter space exploration

Comprehensive network: The parameter exploration focussed on finding suitable parameters to generate the desired behaviour. In the first phase we focused on the CPG dynamics alone (see table 3). This resulted in 3750 simulations.

In the second phase we explored 34 phenotypes (we define genotype within this pa-

per as the combination of the possible parameters, and the phenotype as the resulting movement pattern, which a particular parameter combination generates), which produced the most interesting CPG behaviours from the first phase (increasing Flip-Flops with increased input). Therefore ultimately in the Comprehensive network we only explored different weights from the inhibitory neurons to the rotation neurons (w_{IIL} , w_{ICL}), tuning for the desired rotation behaviour. The weights explored were: -1, -2.6, -4.1, -5.7, -7.2, -8.8, -10.3, -11.9, -13.4, -15, leading to 100 simulations per phenotype, resulting in 3,400 simulations.

Core network: We ran a 2,000 timesteps simulation for 4 adaptation related neuron parameters and 4 weights, w_{EI} , w_{EO} , w_{II} , and w_{IO} , each with 5 values, resulting in 390,625 simulations (see table 1). Each genotype then was run five times, where the input strengths were given at a constant 25%, 50%, 75% and 100% symmetrically, and an asymmetrical combination of 25%/100% input (which should result in a right turn).

Unsuccessful simulations were excluded, those were chosen by these constraints:

- 1. The CPG layer produced less than 2 spikes (no Flip-Flopping with symmetric input) in both the Core and Comprehensive version
- Output neurons produced maximally > 60 spikes/s (Core) or 120 spikes/s (Comprehensive)

If any of the 5 simulations for each genotype would fall under these two conditions, the whole genotype was deemed unsuitable.

4.2.5 Trajectory Analysis

We were mostly interested in the embodied behaviour of the CPG, we focussed the analysis on the zig-zag behaviour (frequent and evenly length of change of the steering direction) of the agent's trajectory. We subdivided the trajectory into segments which depict the transition from a left turn to a right turn and vice versa (Figure 4.3b). The trajectory formed by these segments we dubbed the underlying trajectory. We excluded turns smaller than $1 \cdot 10^{-3}$ rad/ms, which we regarded as low-level noise.



This segmentation then enabled us to analyse the stability and sinuosity of the

Figure 4.3: **Trajectory-Analysis.** A) Top: A simulated trajectory. Bottom: The trajectory's angular velocity profile. B) An underlying path, where each segment connects to the positions of left and right turning transitions. C) Measures of sinuosity: the length difference between the path and the underlying path in each segment, the number of segments and the length of each segment. D) Measures of stability: Overall movement direction and intersegment angle.

trajectory (Figure 4.3c, d). As the measure of sinuosity we regarded the length difference between the actual trajectory and the underlying trajectory. The bigger the difference, the curvier the actual trajectory is between transitions. Additionally, we used the number of transitions per trial, as well as the length of the segments (Figure 4.3c). As a stable trajectory we defined trajectories which did not change in heading over time, thereby using the angle between the first and last segment (Figure 4.3d). Additionally, we analysed the inter-segment angles and the whole trajectory angle.

Comprehensive network: In the first phase (CPG exploration) we focused solely on the number of switches to increase with input. In the second phase (inhibitory neurons to rotation neuron weights), we analysed all 3400 phenotypes visually.

Core network: We restricted the search to the following conditions, which would most likely contain the phenotype we were searching for (less zig-zags, but curvier with less input and more zig-zags, but straighter with high input):

- Sinuosity: it should decrease with input, while the number of transitions should either increase or disappear (smooth trajectory), and the length of the segments decrease or disappear.
- 2. Stability: Median intersegment angle between \pm 0.1 rad, the first to last segment overall angle between \pm 0.25 rad and the trajectory angle \pm 0.25 rad as well.

| $w_{EI}, w_{EO}, w_{II}, w_{IO}$ | $g_{adapt}[S]$ | A[unitless] | p[unitless] | $	au_{adapt}[\mathbf{S}]$ | |
|----------------------------------|----------------------|-------------|-------------|---------------------------|--|
| 0.5 | $0.25 \cdot 10^{-7}$ | -7 0.01 1 | | 0.05 | |
| 1 | $0.5 \cdot 10^{-7}$ | 0.05 1.5 | | 0.1 | |
| 2 | $1 \cdot 10^{-7}$ | 0.1 | 2 | 0.2 | |
| 3 | $2 \cdot 10^{-7}$ | 0.2 | 3 | 0.3 | |
| 4 | $4 \cdot 10^{-7}$ | 0.5 | 4 | 0.5 | |

Table 1: Core network. Parameter values used in parameter space exploration.

| E[A] | I[A] | O[A] |
|------|------|-------------------------|
| 0 | 0 | $3.769810 \cdot ^{-10}$ |

Table 2: Core network. Constant current offset values for different neuron types

| w_{AI} | $g_{adapt}[S]$ | p[unitless] | A[unitless] | $	au_{adapt}[\mathbf{S}]$ |
|----------|----------------------|-------------|-------------|---------------------------|
| -7 | $0.25 \cdot 10^{-7}$ | 0.01 | 1 | 0.05 |
| -8 | $0.5 \cdot 10^{-7}$ | 0.05 | 2 | 0.1 |
| -9 | $1 \cdot 10^{-7}$ | 0.1 | 3 | 0.2 |
| -10 | $2 \cdot 10^{-7}$ | 0.2 | 4 | 0.3 |
| -11 | $4 \cdot 10^{-7}$ | 0.5 | 5 | 0.5 |
| -12 | | | | |

Table 3: Comprehensive network. Parameter values used in parameter space exploration.

| E[A] | V[A] | IL[A] | CL[A] | A[A] | I[A] |
|------|--------------------------|-------------------------|-----------------------|------|------|
| 0 | $1.22510 \cdot 10^{-10}$ | $5.5125 \cdot 10^{-11}$ | $1.05 \cdot 10^{-10}$ | 0 | 0 |

Table 4: Comprehensive network. Constant current offset values for different neuron types

4.3 Results

4.3.1 Comprehensive Network

Our initial aim was to develop a SNN representing Comprehensive knowledge of LAL neuron types and putative functions (Steinbeck et al., 2020a). The resultant Comprehensive model (see Figure 4.2a) is represented by 12 neurons and 7 parameters. The model consists of two logical divisions: motor control neurons and CPG neurons. The input neurons (E) feed into the motor control neurons, which in turn feed into the ipsilateral actuator (IL for turning, V for velocity) and the contralateral actuator (CL for turning). The velocity neurons furthermore feed into the CPG neuron pathway (see supplementary figure 4.8).



Figure 4.4: **Trajectory Phenotypes.** A) We found 6 common phenotypes. I. Zig-zag, II. Curve, III. Straight, IV. Loop, V. Chaos and VI. Stopping. B) The zig-zag phenotype we further divided into 7 subcategories. a: The change in trajectory from low input to high input is reflected in less pronounced Zig-Zagging (desired), b: the reverse, c: where the agent loops with low input but zig-zags with high input, d: asymmetrical Zig-Zagging (which behaves as a) otherwise), e: curvaceous Zig-Zagging, f: just Zig-Zagging and g: noisy Zig-Zagging.

To validate that the model can produce the two adaptive motor patterns that the LAL needs to produce we explored a focused region of the parameter space. The parameter space consisted of the adaptory current parameters (4) and the weights W_{IIL} , W_{ICL} and W_{AI} , connecting the inhibitory neurons with the contralateral descending turning neurons and the adaptory neurons to the inhibitory neurons. Out of 3750 parameter combinations (genotypes), we chose 3400 with the most interesting CPG behaviour, defined as the increase in switching behaviour with increased input (see Figure 4.4). Further characterisation of the 3400 genotypes, showed the following phenotype distributions: zig-zag (86.47%), straight(11.44%), curve(1.12%), loop(0%), chaos(0.88%) and stopping(0%). Within Zig-Zagging, we further divided 7 sub-phenotypes (Figure 4.4b, percentages scale to 2761 zig-zag phenotypes):



Figure 4.5: **Behaviour of the Comprehensive network in response to different sensory inputs.** A-D shows the network activity during a simulation run with the resulting trajectory below (for neuron types see figure 4.2). A) Low symmetrical input leading to strong Zig-Zagging. B) High symmetrical input leading to minimal Zig-Zagging with forward motion. C) Asymmetrical input leading to circling. D) Changing input from medium to high symmetrical input (asterisk * indicating the time point of input change in both the neural trace and in the motion trace) leading to firstly Zig-Zagging to forward motion. The trajectories for C & D are scaled to 50% in relation to A & B.

curvier with low input to straighter with high input Zig-Zagging (34.63%), straighter to curvier Zig-Zagging (4.69%), curvaceous Zig-Zagging (19.52%), asymmetric Zig-Zagging (0%), curve to Zig-Zagging (0.68%), just Zig-Zagging (7.24%) and, randomly occurring Zig-Zagging (33.23%). The asymmetrical input simulations always resulted in a targeted rotation.

Figure 4.5 shows the adaptive motor patterns that are produced by one parameter combination for a range of sensory inputs. Weak, unreliable inputs produce oscillatory behaviour (see figure 4.5a,d) and clear sensory signals produce turning (figure 4.5b) or fast straight movement (see figure 4.5c). Thus we have existence proof that the Comprehensive network can function adaptively as a steering network and as a CPG generating oscillatory behaviour.

4.3.2 Core network

The network setup generates a variety of movement patterns. Out of the 390,625 phenotypes, 290,886 did not meet the network constraints (the CPG did not spike in each simulation, and the output activity was too high). From the remaining 99,739 phenotypes, 393 [at least 4/6 matching sinuosity and stability conditions] (3,224 with at least 3/6 sinuosity and stability conditions) produced trajectories which met the phenotype measures we were aiming for. We used these exclusion criteria with the logic, that if a desired trajectory is not generated when simulating it once, it will not occur consistently.

We visually judged the generated trajectories suggested by the analysis. We encountered six overall phenotypes of trajectories (Figure 4.4a, percentages scale with 393 + 3,224 suitable phenotypes): zig-zag (76.33%), straight(21.51%), curve(0.0022%), loop(0%), chaos(0.02%) and stopping(0%). Within Zig-Zagging, we further divided 7 sub-phenotypes (Figure 4.4b), percentages scale to 2761 zig-zag phenotypes): curvier with low input to straighter with high input Zig-Zagging (65.85%), straighter to curvier Zig-Zagging (6.7%), curvaceous Zig-Zagging (2.68%), asymmetric Zig-Zagging (6.99%), curve to Zig-Zagging (0.69%), just Zig-Zagging (13.18%) and, randomly occurring Zig-Zagging (3.91%). The asymmetrical input simulations always resulted in a targetted rotation. The network is robust to parameter changes. We ran a principal component analysis (PCA) on the phenotypes to see if a dimension reduction was possible and which of the parameters mostly contribute to the Zig-Zagging phenotype. We used Min-Max scaling or Standardization to treat the parameters. We ran PCAs on 1. All trajectories (\sim 100,000), 2. Only the sensible trajectories (\sim 3,500), 3. All interesting Zig-Zagging trajectories (\sim 400).



Figure 4.6: **Parameter combination relationships producing the desired behaviours in the Core network** with low symmetric input the trajectory is strongly Zig-Zagging, with high input barely Zig-Zagging (see figure 4.4B[a]). A) The heatmaps show the network parameters plotted against each other in pairs. Many of the parameter pairs show clusters of combinations that are more likely to lead to the desired behaviour. B) The web-diagram depicts all-against-all relationships in a digested way: the lines show how the relationship between the parameters should be set up (i.e. one weak, one strong within the range we explored). The colours represent the highest numbers these combinations appeared. W_2 was excluded since the vast majority of successful combinations appeared with the same value.

We did not find a large reduction to be possible in any case; the highest PC1 for all trajectories explained 20% of the variance, and the highest PC1 for the best trajectories explained 26% of the variance. The leads us to believe, that the Zig-Zagging phenotype can occur with many different genotypes of network parameters. We compared different parameter combinations to investigate how big the spread of the best Zig-Zagging is (Figure 4.6a). Most combinations yield a big spread, but some parameter combinations are more likely to produce the desired behaviour. Additionally, changing the noise component to time independent even increased the spread of possible parameter combinations (supplementary figure 4.9).

The network is robust to computational noise. Then we went on to investigate the reproducibility of the generated trajectories. We selected visually the phenotypes which produced the desired behaviour best. Each of those, we ran 100 times. No trajectory generated was the exact same with each repetition. The only term influencing this variable outcome is the additional noise component during the neuronal computation. This component we changed in its magnitude (5-fold higher, 10-fold lower than the original, see Figure 4.7).



Figure 4.7: **Reproducibility of desired behaviours of the Core network with different levels of noise.** We chose 25 parameter combinations which showed great approximations of the desired behaviour (see figure 4.4B[a]) and changed the noise component of the voltage computations (see Methods). Each behaviour was simulated 100 times. The top row shows the number of switches per simulation, the bottom row the mean trajectory angle (the overall trajectory direction from start to end) with different bilateral input strengths (grey lines & blue dots) over 100 simulations. The overall behaviour (mean of all means in red) stayed the same with increased switching from increased input strength, while the variability expectantly increased with increased noise.

We found that this noise component largely determines the overall outcome of the variability of trajectory, which seems to be determined by the phase building up to

the Flip-Flopping behaviour (see Figure 4.2f). Yet, the overall Zig-Zagging behaviour stays the same, meaning the increasing zig-zags with higher input, the overall forward motion.

Designing principles for a zig-zagging agent In order to build a CPG model in a Braitenberg configuration as shown, the most important parameter relationships are: The adaptory conductance increase due to previous spiking G_{astep} , the adaptory conductance time constant G_{aTau} , the weights from the inhibitory neurons to the other inhibitory neurons w_{II} , and to the output neurons w_{IO} should be strong, the adaptory conductance G_a rather strong, while the weights from the input neurons to the inhibitory neurons w_{EI} and to the output neurons w_{EO} and Ga_{power} should be rather small within the range we explored (Figure 4.2b).

- CPG behaviour: the build-up of the adaptation should be slow enough for the agent to actually be able to steer around for weak inputs, but fast enough to not steer much when receiving strong inputs. The power term therefore may lead to too fast build up.
- Setup Braitenberg: the actuation difference between left and right achieved should be high, so that the force generation difference is big enough to steer. Therefore the connection from the inhibitory neurons to the output neurons should be strong.

4.4 Discussion

4.4.1 Takehome message

We set out to explore how a neural network could produce adaptive behaviour in a navigation setting. We built the spiking neural networks based on the overarching layout of the LAL and the behaviours it should produce (Steinbeck et al., 2020a). We chose the networks to keep a hemispheric layout, while simultaneously containing a

CPG. A non-symmetric input resulted in a non-symmetric output, while symmetric input generated searching behaviour for lower input strength and forward movement for higher input strength. Therefore, if a reliable stimulus appeared towards one side, the agent would steer towards it, whereas if it appeared ahead, the agent would approach it directly, similarly as phonotaxis in crickets (*Gryllus bimaculatus*, Zorović & Hedwig (2013)). If the sought stimulus would not be perceived though, the agent would generate small scale search motifs, similarly to the Zig-Zagging in silkmoths (*Bombyx mori*, Kanzaki et al. (1992)).

There are many different combinations of neuron parameters and connection weights leading to the desired behaviour, even with varying amounts of noise, indicating that the network's setup may be well suited to generate this kind of behaviour. The network was capable of generating a range of other naturalistically resembling movement patterns, indicating that this network anatomy can be easily adapted to generate different adaptive behaviours.

4.4.2 Flip-flop mechanisms

How do the inhibitory neurons switch between higher and lower firing rates? We choose the Flip-Flop mechanism to be an intrinsic adaptation, which is only driven by the reliability of a navigation relevant stimulus. This way, the mutual inhibition will lead to a CPG behaviour and the Flip-Flopping will only occur if the neurons are activated simultaneously with a similar strength.

The bilaterally similar input strengths leading to a Flip-Flop behaviour emerged in the network as described by Adden et al. (2020) as well. Their rate based model has morphological similarities to our model. However, the Flip-Flop driving mechanism is a hardcoded inhibition of spike rate, if the opposite population of neurons enters a high spike rate. This type of switching is inspired by bi-stable neurons which have low-firing states and high-firing states they can switch between (Gruber et al., 2003). Set into a navigation task, this model reproduces olfactory tracking behaviours and path integration behaviours.

In our Comprehensive network we investigate the interaction between the Ventral Protocerebrum (VPC) and LAL (Iwano et al., 2010). This bidirectional connection seems to be established by unilaterally descending and ascending neurons. The Flip-Flopping of Type I may be a result of preceding network activity, and not being the neuron type which produces the Flip-Flopping by itself. This would make sense as Type I neurons directly project towards the motor centres. If Type I neurons would be responsible for both initiating steering and Flip-Flopping, the species of insects (moths) which use a kind of Zig-Zagging, would zig-zag continuously to a stronger or lesser degree, based on our model. While some species of ants seem to continuously zig-zag while navigating (Le Möel & Wystrach, 2020), silkmoths only Flip-Flop when tracking pheromone plumes. Therefore we chose the adaptation neuron to be the ascending Type II neuron coming from the VPC, which innervates the inhibitory Type III neurons in the LAL, which in turn inhibit the contralateral Type I neurons.

In our Core network, Flip-Flopping occurs as a result of integrating the input neurons' activity and simultaneous mutual inhibition by Type III neurons, which are intrinsically adaptative.

Other pathways may influence the Flip-Flopping mechanism in moths, one of them being optic flow (Pansopha et al., 2014). The moths alter their behaviour, if the optic flow direction matches the expected direction, but the extent of perceived OF increases or decreases their turns. If the optic flow does not match, the moths perform a stereotyped pattern Therefore, we suggest the adaptation mechanism to be partly be driven by external stimulus like optic flow. Incorporating optic flow to directly con-

trol the adaptation mechanism may increase spatial reliability of the CPG mechanism as it would be linked to external orientation stimuli. Furthermore, modulatory inputs to the LAL may alter the LAL's function depending on the agent's motivational state (Manjila et al., 2019). This could function as a "switch" to activate/deactivate specific functions within this network (maybe the CPG subnetwork) or deactivate the LAL as a whole.

4.4.3 What do the output neurons encode for?

Which kind of information is actually sent to the motor centres? In the Core network we simulated the outputs to the motor system to act similarly as a Braitenberg-vehicle, where we pick up on the observation that steering is initiated due to an imbalance of neuron activity between hemispheres (Iwano et al., 2010; Zorović & Hedwig, 2013).

In the Comprehensive network we suggest a split into turning and velocity neurons due to optic flow integration in descending neurons in bees and the latest discoveries in the descending neurons of *Drosphila*. Descending neurons have been shown to innervate different groups of muscles: while some groups target muscle groups which are more involved in power generation, others target muscle groups which are more involved in steering (Namiki & Kanzaki, 2018). Unilaterally descending neurons in *Drosphila* have been shown to code for velocity (Bidaye et al., 2020). Some of unilaterally descending neurons show bilateral innervation of the motor centres (Bidwell & Goodman, 1993). Functionally, this could control walking velocity across both sides of the motor centres. Other Type II neurons have been shown to be involved mostly in steering (Zorović & Hedwig, 2013; Iwano et al., 2010; Namiki & Kanzaki, 2016). Animals (insects) steer their bodies while walking by pushing the outward actuators away from the body while pulling in the actuators on the inside (Mantziaris et al., 2020). Both actuator centres therefore can produce both left and right turns
individually. Fiore et al. (2017) suggested a similar pre-motor command structure (walking forward, left and right in both LALs), yet more abstract than our Comprehensive model. The biggest difference to our models is the assumption that the LAL neurons are inhibited by CX neurons (Fiore et al., 2015).

However, evidence suggests that the meta-motor commands could be more nuanced than this. In cockroaches, recording of CX neurons show how different units encode for different walking directions and velocity (horizontal representation) (Martin et al., 2015). In flying insects like bees, different descending neurons are activated by different directions and velocities of optic flow, therefore coding for pitch, roll and yaw (vertical representation) (Goodman et al., 1987; Ibbotson, 1991; Bidwell & Goodman, 1993). This could mean that motor commands are encoded in a 3-dimensional vector space, where a neuron encodes for a specific movement direction in an idiosyncratic manner, as well as the velocity into that direction. Therefore, motor command encoding could possibly be representing walking movements and flying movements separately, or when in either state, only a subset of all possible motor commands could be active.

Another question is how both the left and right descending commands are coordinated. While for a rotation an imbalance of activity between left and right may be sufficient to initiate rotational movements (steering), how are translational movements coordinated? We know from both walking and flying insects that these movements are used (Ravi et al., 2019). This would point towards an identical motor command representation in both pairs of the LAL, where both hemispheres encode omnidirectional movements and velocities, and the consequent motor group innervations are mirror symmetrical.

4.5 Conclusion

We have investigated the network dynamics of a spiking neural network model inspired by the Lateral Accessory Lobe of the insect brain. The network dynamics produce a stimulus reliability dependent small scale search behaviour. This enables the network to generate in a transient fashion anything between targetted steering responses and Zig-Zagging responses, which is dependent on the input strength and input source. That Zig-Zagging behaviour can be (re-)produced with a large variety of parameter combinations and noise levels, speaking of a robust network design. Furthermore, other generated behaviours resemble naturally occurring behaviours of navigating animals. These characteristics makes this network an ideal candidate for modelling Zig-Zagging behaviours, with the Zig-Zagging being generated by internal dynamics (as opposed to resulting from external stimulus changes).

In preliminary simulations we investigated the network in a simple navigation setting (Steinbeck et al., 2020a). We found that the generation of small scale search movements, which are directly modulated by the reliability of sensory signals, can improve the success of approaching a target. In future studies we want to incorporate this model with more complex visual stimuli (Risse et al., 2018), other modalities and additional modalities like optic flow (for the CPG adaptation mechanism Pansopha et al. (2014) or optomotor response Bidwell & Goodman (1993)) or olfaction (Ando et al., 2013) and navigation models (Sun et al., 2020; Le Möel & Wystrach, 2020). Ultimately, this type of stimulus reliability actuator control can improve autonomous agent navigation, as it designed to adapt to changing stimuli and therefore may lead to greater stimulus detection capabilities.

4.6 Supplementary figures



Figure 4.8: **Comprehensive network: Central Pattern Generator pathway.** A) The left-hand pathway. The velocity neuron V drives the adaptory neuron A, which in turn drives the inhibitory neuron I. *I*'s output then inhibits the contralateral descending neurons. B) The right-hand pathway.



Figure 4.9: **Parameter combinations using a different noise component.** Parameter combination relationships producing the desired behaviours in the Core network with independent noise; with low symmetric input the trajectory is strongly Zig-Zagging, with high input barely Zig-Zagging (see figure 4.4B[a]). A) The heatmaps show the network parameters plotted against each other in pairs. The parameter pairs show clusters of combinations that are more likely to lead to the desired behaviour. B) The web-diagram depicts all-against-all relationships in a digested way: the lines show how the relationship between the parameters should be set up (i.e. one weak, one strong within the range we explored). The colours represent the highest numbers these combinations appeared.

5 Chapter 4: A Bilateral Vision approach to View-based snapshot navigation.

This chapter was written and the experiments designed and executed by FS. PG,TN and AOP supported with the experimental designs and editing. EK and AD helped with setting up the Antworld pipeline.

Abstract

Panoramic images have been used successfully in the recovery of orientation for visual place recognition navigation tasks. Inspired by insects using two eyes and the brain structured into two hemispheres we investigated, how two independent, non-panoramic images can be used. The visual scene was divided into two Fields of View and the images were memorised at an angle where each eye is facing the desired direction independently, the angle we called the Offset. The queried images then were compared to the memorised images, eye per eye. We found that when following a route, calculating the Familiarity difference between both Fields of View at an Offset indicates a steering direction to recover the desired direction. When rotated away towards the left of the desired heading direction, a right turn would be indicated, and vice versa. The success rate increases with increasing Fields of View and a non-zero Offset. The most correct steering responses towards the desired heading direction occur around the Offset. This mechanism's efficacy does not deteriorate with decreased visual resolution on-route, but only minorly off-route, when considering aliasing. Thereby we show how an orientation can be recovered without the need to scan the entire panorama, but by using the familiarity difference between two Fields of View only.

5.1 Introduction

Visual navigation algorithms have seen increasing usage in the past decades, as they present a cheap way to provide egocentric spatial information for application in autonomous agents. Effective visual navigation algorithms enable autonomous agents to explore and navigate environments without external control. One successful approach to apply vision to navigation is Simultaneous Localization and Mapping method (SLAM, Smith1986). This approach often leverages feature extraction paradigms, which identify, track and locate visual navigation relevant features in an agent's environment (Chen et al., 2021; Gridseth & Barfoot, 2021). In parallel, the state of that agent is estimated, so that it may navigate within that environment. This process guickly becomes computationally expensive, for complex or large environments, which both increases power consumption and decreases the ability to provide real-time solutions. Therefore, using this method on an truly autonomous agent (as in one with no external computation) may be a limiting factor (Bresson et al., 2017). Contrary to this top-down engineering approach, insect inspired view-based navigation models have seen increased attention, as these derive from agents with poor visual resolution (1°-4°, Schwarz et al. (2011)) and computationally restricted hardware (ants have less than \sim 500,000 neurons in their brain, (Godfrey et al., 2021). Thus, mimicking insect behaviours and computational principles may overcome hardware limitations and increase not only computational efficiency, but also the robustness of applied navigation mechanisms in a dynamic environment.

Behavioural experiments and modelling of visual landmark learning in bees (Cartwright & Collett, 1983), has sparked the subsequent development of several view-based navigation algorithms. With view-based navigation, an environment can be sparsely represented with reference images (snapshots) taken at nodes relevant for navigation within this environment (Franz, 1998). Simple visual algorithms can be used to navigate between those nodes. For instance, navigation to a node can happen via gradient descent, as the image difference can be used as an indicator for proximity to a goal location (Zeil et al., 2003). By calculating the root mean square pixel difference between panoramic snapshots and currently displaced images (query images) in the

vicinity, a spatial Image Difference Function (IDF) can be established. This function is minimal when the query image is in the same location as the snapshot, but gradually increases with distance to that snapshot's location. By following the descending gradient, the location of the snapshot can be found.

The measure of visual difference can directly be incorporated into an algorithm for setting orientation as part of homing algorithms. One set of methods uses the concept of a 'visual compass' (Labrosse, 2006; Zeil et al., 2003) which is a method to find the rotation between a snapshot and a query image, therefore leading to the discovery of the direction of the snapshot. This method resembles the behaviour of ants which scan the environment with body rotations while visually navigating (Lent et al., 2010; Wystrach et al., 2014). Thus, a rotation can aid in finding the same orientation as the goal snapshot's. Another option for view-based navigation is to employ a strategy that reduces the displacement of landmarks in the query image in comparison with the snapshot in order to navigate towards snapshot locations (Franz et al., 1998). Similar methods use image interpolation (Chahl & Srinivasan, 1996) or matched-filtering (Möller & Vardy, 2006) to navigate towards snapshot locations. Using snapshots to define single locations can be used as the basis for routes and maps (Franz, 1998; Stürzl et al., 2008; Zeil, 2012). Insect inspired Snapshot Navigation algorithms primarily focus on route navigation behaviours of Hymenoptera (Narendra, 2007; Philippides et al., 2011; Collett et al., 2013), where routes can be established by taking several snapshots along a path to be navigated along. This way, each snapshot represents an intermediate goal location which can be navigated towards; linking several together, larger distances can be traversed (Smith et al., 2007). Those snapshots can be stored either as they are ('Perfect Memory') or by feeding them into a holistic memory creation mechanism, such as the machine learning algorithm 'Infomax'. The Infomax algorithm creates one holistic memory from all snapshots, memorizing effectively the most different snapshots from the whole set of snapshots (Baddeley et al., 2012;

Wystrach et al., 2013). This reduces the required storage capacity, especially for big snapshot sets, as the number of 'neurons' equals the amount of pixels that the visual system uses. However, this may come with the trade-off of lower accuracy (Husbands et al., 2021).

Insect inspired Snapshot Navigation algorithms work in a stop-scan-go fashion. Panoramic snapshots are taken along a route, where the heading of the snapshots aligns with the direction towards the next snapshot location. After memory formation, the agent is released in the vicinity of the route. In its location, the agent performs a 360° rotation, and at each rotation step compares the query image with the snapshots, calculating a rotary Image Difference Function (rIDF). The rotation at which the rIDF is minimal, the agent will move one step and repeat this procedure. This reduces the effort of navigation from locating oneself in a global reference system to a simple action, where the direction to be taken is implicit by following the highest visual familiarity (Baddeley et al., 2012).

Algorithms that rely on whole-body rotation or mental rotation (Möller, 2012) to evaluate possible directions of travel can be computationally or time intensive. Therefore, it is interesting to look in detail at the Active sampling behaviours of insects to make Snapshot Navigation even more efficient. Based on the observation that ants move in sinusoidal trajectories, Kodzhabashev & Mangan replaced the stop-scan-go movement strategy with a sinusoidal movement pattern, where the amplitude is modulated by the snapshot familiarity. This leads to a high amplitude sinusoidal movement with weak input familiarity and a shallow sinusoidal movement with strong familiarity, enabling a robot to navigate along a route (Kodzhabashev & Mangan, 2015). Therefore, the scanning movement is spread out over several movement steps and makes the familiarity following process more dynamic. Furthermore, recent advances in insect neuroscience have inspired other ways in which view-based navigation models can be implemented efficiently. In regard of visual memory, the Mushroom Bodies (MB) have been identified as a structure capable of forming memories of visual stimuli (Liu et al., 1999; Vogt et al., 2014; Buehlmann et al., 2020; Li et al., 2020). A plausible model of how MBs might implement visual memory for navigation comes from Ardin et al. Visual projection neurons connect randomly to a 2nd layer, where each 2nd layer neuron needs activation of multiple inputs to fire. These converge then onto one extrinsic neuron, which introduces a reinforcement signal, therefore associating certain inputs to a certain 2nd layer activity. This leads to a measure of familiarity. The number of neurons determine the capacity of this network, scaling the capacity logarithmically. Using this type of memory in a Snapshot model generates comparable performance as a perfect memory or Infomax algorithm. (Ardin et al., 2016)

Insect neuroscience has also provided us with a detailed understanding of another brain area important for orientation and spatial control. The Central Complex (CX) is a conserved brain structure which receives multimodal inputs (Heinze et al., 2013). It is involved in spatial orientation such as compass driven behaviours (Cope et al., 2017; Pisokas et al., 2020; Dan et al., 2021) and may also play a role in view-based navigation in ants (Wystrach et al., 2020b). The CX receives MB outputs, and might be used to maintain a course that has been set by visual information (Schwarz et al., 2017).

One of the sub-structures of the Central Complex is the Lateral Accessory Lobe. The LAL is a conserved brain structure, which receives inputs from all navigation relevant brain areas except reflexive pathways and connects with the motor centres. It consists of two lobes, one located in each brain hemisphere. The inputs are largely divided hemispherically, meaning that the inputs towards one lobe originate mainly originate

in the same hemisphere (Namiki et al., 2014) and subsequent processing occurs predominantly within the same hemisphere also (Paulk et al., 2015). Behaviourally, the LAL seems to be involved in the generation of small scale search behaviours (Kanzaki et al., 1992; Pansopha et al., 2014). These seem to be modulated by the reliability of navigation cues, leading to extensive search for a cue if that cue is weakly perceived, and targeted steering behaviours when the cue is strong (Namiki & Kanzaki, 2016; Steinbeck et al., 2020a). Steering is achieved by an imbalance of activity of descending neurons towards the motor centres (Zorović & Hedwig, 2013; Iwano et al., 2010; Rayshubskiy et al., 2020). Consequently, we have recently developed a steering framework based on the LAL (Steinbeck et al., 2020a), which provides a general mechanism for sensory information to control orientation and active search.

Based on the steering framework, where hemispherically divided inputs ultimately lead to a steering response, we investigate how bilaterally organised visual memories could achieve a steering response to navigate along a learned route. Instead of using a single panoramic image as a memory, as for many of the models above, we will use two lateralised memories. This is biologically plausible given the lateralised wide field eyes and the bilateral MBs.

Given the LAL controls steering by using the reliability of lateralised sensory inputs, we ask how the organisation of bilateral view-based memories can be be optimised to provide a reliable steering signal. The investigation mainly focuses on the Field of View (FoV), which describes how much raw visual information is available to each hemispheric memory, and an Offset, which describes the target/familiar orientation of the stored memories in relation to the agent's heading (Wystrach et al., 2020b). The spontaneous difference in visual familiarity between the current and stored views for both hemispheres is used as a steering signal, similar to a taxis mechanism. In sum, we explore which type of visual system would fit best with this steering process and therefore would be a biological plausible input to the insect LAL during navigation.

5.2 Methods

Simulations and analyses were performed using Matlab 2019a (MathWorks, Natick, MA, USA) and Python 3.

5.2.1 Antworld Image Rendering

For the exploration for Bilateral Snapshot Navigation we chose to use the "Antworld" virtual environment, which is a LiDAR (Light Detection And Ranging) 3-D reconstruction of an experimental location, near Seville Spain, which has been used for observations and experiments with *Cataglyphis velox* ants (Risse et al., 2018).



Figure 5.1: Visual environment "Antworld" simulating a desert-like environment with sparse vegetation. A top-down view on the virtual environment (A), showing the route taken (red), with the displaced test locations along parallel paths (blue) and the off-route test locations (green) (D). The two locations singled out show the view on route (B) and parallel off route (C) at different visual resolutions.

Within this environment we chose two routes which closely resemble real routes taken by ant foragers navigating towards their nest (routes 3 and 12 from the BoB robotics GitHub, figure 5.1 A). The rendering of the test images is done with the BoB robotics Antworld rendering pipeline. To generate training views and displaced test locations, on each route we chose 31 equally distant locations, where the heading angle faces directly towards the next location. These are the training locations for the snapshots. For testing, at each location we rendered five off-route locations normal to the route direction, both to the left and right (distances were 5, 10, 30, 100, 300 mm; figure 5.1 D). The panoramic images are rendered so that the centre pixels represent the heading direction, i.e. the view orientation oscillated about the overall route direction. To investigate how bilateral view familiarity differences might interact with basal sinusoidal paths, we selected one route segment and rendered seven positions along a spatial sinusoidal trajectory with an amplitude of 3cm and a wavelength of 10cm (Graham & Collett, 2002).

5.2.2 Field of View

The Field of View (FoV) describes the visual input available to each hemisphere (in the sense of eyes), which is then both used for snapshots and the comparison of the query images to the snapshots to generate the rotary Image Familiarity Function (rIFF). Because both hemispheres/eyes have a field of view, visual systems are further described by the degree of visual overlap β (the visual range of both eyes overlapping in the front) and the size of the rear blindspot γ (how much visual range is missing to the back). The panoramas central horizontal pixel is the heading direction, therefore the blindspot γ refers to how many pixels are taken away from the sides, and the overlap β defines how many pixels are designated to be taken beyond the horizontal centre contralaterally for each of both final hemispheric images.

| Overlap β [°] | -180 | -90 | 0 | 90 | 180 | 270 | 360 |
|------------------------|------|-----|-----|----|-----|-----|-----|
| Blindspot γ [°] | 0 | 90 | 180 | | | | |

Table 5: Overlap and rear Blindspot values.



Figure 5.2: View parameters for binocular visual navigation. For each navigation test the visual system and stored visual memories are defined by three parameters. Left: Each eye has a field of view, which is defined by a region of binocular overlap β at the front of the simulated ant and a blind-spot γ to the rear. Right: An Offset parameter α defines the orientation, relative to the direction of the training route, at which the maximum familiarity shall occur.

5.2.3 Offset

The Offset α describes the orientation of a stored snapshot in relation to an agent's body and to the overall route direction. If a view is stored with no Offset this would mean that the most familiar direction being directly aligned with the agent's overall direction of travel. An Offset angle for each hemisphere would result in maximum familiar directions which occur at angles symmetric to the agent's centre line. For example, an Offset of 45° would result in the left eye/hemisphere having a maximum familiarity when the agent was rotated by 45° to the right from the original heading direction and the overall route direction from the training images, and for the right hemisphere rotated by 45° to the left (figure 5.3, D & E grey). For the convenience within the setup of this experiment, this is achieved by rotating the panoramic query image for each hemispheric query image before cutting it into the FoV. The Offset values were $\alpha = [0, 9, 18, 27, 36, 45, 54, 63, 72, 81, 90]$.

5.2.4 Image Processing

The rendered panoramic images dimensions are 720x150. First, the Sky is whitened and then the whole image converted to gray-scale. Each image then is cut into two views, depending on FoV. For our tests on the impact of resolution, images are downsampled to a 90x10, 60x8, 30x6, 20x4 and 10x2 resolution using MatLab's imresizefunction and for the main analysis we use 90x10, which gives a resolution comparable to the visual resolution of the ant compound eye.



Figure 5.3: **Impact of Offset on visual familiarity.** For one set of visual parameters at two locations, we show how an offset on the stored views impacts on view familiarity. Panoramas from two locations (A), are investigated for (B) a visual system with 180° field of view for both eyes (C, no overlap or binocular region). (D,E) visual familiarity of the current view relative to the stored view for different headings. The top depictions show the Offset both in terms of spatial rotation (ant) and the snapshot shift within the entire panorama. Whereas with no Offset the left memory (yellow) should be perceived in its original orientation (left), an Offset of 45° shall result in a shifted visual location (right). In the upper panels the familiarity scores per heading of the left eye (yellow) and the right eye (blue) are shown, where 100% familiarity comes when the current view is at the same heading as the stored view. With an Offset of 45° (D & E grey), the IFF_{max} of both hemispheres will appear in the heading direction. With an Offset of 45° (D & E grey), the IFF_{max} of the left hemisphere will appear with the agent rotated 45° to the right and vice versa. D & E lower: the familiarity difference between left and right eyes. D gives examples where the familiarity difference would give a good steering signal across most headings, whereas in E the difference would not give good steering information.

5.2.5 Rotary Image Familiarity Function

The Rotary Image Familiarity Function (rIFF) is used to systematically compare a snapshot with a series of rotated versions of the 'current' query image in order to find which orientation gives the most familiar view. The query image is rotated in steps through 360°, at each rotation step (3° for the largest image size, 1 pixel step for the smaller image sizes) the views for both eyes are extracted from the full panorama and then, with the given FoV, the Covariance (familiarity) of each eye's query image is calculated given the ipsilateral snapshot. The off-route query images are compared to the on-route snapshots they lie normal to. Plotting the Covariance for the whole 360° gives the rIFF, one for each hemisphere (figure 5.3).

5.2.6 Measures of successful steering

Here, the displaced off-route images are compared to the on-route images at the nearest location. At each location, the rIFFs of the left hemisphere and right hemisphere are normalised to the $max - 105\% \cdot min$ percentile before being subtracted from each other. This gives us a familiarity difference between left and right eyes which can be used to drive a steering response. Positive values suggest a leftwards turn and negative values indicate steering rightwards, examples where the familiarity difference gives a correct steering response are given in figure 5.3 bottom.

In order to assess the overall success of a given set of visual system parameters, we take the proportion of orientations, across all test locations, where the Left-Right difference in visual familiarity would precede the correct turn response. We initially look at this for all orientations, i.e. for $\pm 180^{\circ}$ from the 'correct' direction (figure 5.4 right). However, given that the main focus of this paper is to consider how a bilateral familiarity metric can work for route guidance, given the way that the insect LAL brain region modulates motor behaviour between steering when sensory signals are

strong, and search when signals are weak. Therefore, for much of our analysis we focus on the proportion of orientations at displaced locations that give correct steering responses, but only with $\pm 90^{\circ}$ from the overall 'training' route direction. This gives us an appreciation of how likely the bilateral familiarity information would be in keeping an agent on the desired route, rather than relying on a search behaviour (see introduction).

5.2.7 Evaluation of aliasing

When asking how bilateral familiarity measures might provide information to drive steering, we look at the likelihood of deriving the correct steering response when the views from displaced locations are compared to the nearest training/stored view from the target route. Real world agents might not have access to information that could ensure they compare their current view to the 'correct' training view. To analyse how aliasing might impact on overall performance, we looked at how aliasing might increase when an off-route test image is compared with all possible on-route snapshots. The aliasing metric is derived by considering which of the stored training views gives the best match for the current location across all orientations and all possible stored views. This gives us a number for the difference in sequence location between the accurate location and the position of the best match. A score of 2 would mean that the best match was 2 positions away from the correct stored image location in the training route sequence of views.

5.3 Results

5.3.1 Overall performance of a bilateral visual familiarity method

Our primary goals for this analysis were to give proof of concept that bilateral visual familiarity information can be used to generate a steering signal and then to investigate how performance depends on the precise organisation of the visual fields and visual memories. The headline result is that a simple Left-Right difference in familiarity can drive steering for a range of locations that are displaced from training positions, and also for a range of orientations relative to the overall route direction.





Figure 5.4: **Steering performance evaluation.** For all visual systems (x axis) and offsets (y axis) we aggregate the tests from all routes, displaced test locations and orientations. We then show the proportion of these tests (n = 310 locations * $180^{\circ}3^{\circ}$ rotations = 18,600) where the familiarity difference would give the correct steering response. Left, we evaluate $\pm 90^{\circ}$ of orientations relative to the overall route direction. Right, for every test location all orientations ($\pm 180^{\circ}$) are evaluated. Top row shows the % correct steering responses on a scale from 0-100, the bottom row from 0-50. The red-spectrum colours indicate a performance of at least $80^{\circ}(left)/30^{\circ}(right)$, the green/blue-spectrum colours indicate at least $75^{\circ}(left)/25^{\circ}(right)$ performance.

In our first analysis, for all orientations at each test location, we evaluate whether the difference in the familiarity between the left and right visual field would lead to a correct steering response. This performance is only just better than chance when taking into consideration all directions ($\pm 180^{\circ}$ to the heading direction) (figure 5.4). When taking into consideration the directions $\pm 90^{\circ}$ to the heading direction, 43 out of 165 (26%) visual system combinations at 720x150 resolution performed over 75% (figure 5.5A). On average, a higher FoV and a medium Offset produces a correct steering response (at least 75%) for most directions ($\pm 90^{\circ}$ to the route). A correct steering response occurs most often around the Offset angle (figure 5.5C).



Figure 5.5: **Steering performance for visual system combinations.** A : The proportion of headings where the Left-Right familiarity difference results in a correct steering response for all Field of Views (x-axis) and Offsets (y-axis). The score is an average for all off-route locations along the route, with each route analysed for in both directions. The regions of high success are highlighted in Magenta = 80% performance or Cyan = 75% performance. B: For the best performing visual systems we take a more detailed look at how performance varies with Offset. C: Detailed angular steering response. Left: For FoV 90 $^{\circ}$ 90 $^{\circ}$ on route 3, the amount of correct steering responses in relation to the original heading direction amongst all Offsets are shown. All Offsets colourcoded with the labels as indicated on the very right, with the dotted arrows indicating the Offset directions. Three Offsets are shown individually towards the centre & right.

5.3.2 Visual resolution

Reducing the visual resolution increases the performance of correct steering responses. 45 out of 165 (27%) visual system combinations performed over 75% with 90x10 resolution, 53 out of 165 (32%) with 60x8 resolution, 56 out of 135 (41%) with 30x6 resolution, 45 out of 90 (50%) with 20x4 resolution, 34 out of 60 (57%) with 10x2 resolution.



Figure 5.6: **Steering performance relative to resolution.** For both Route 3 (Left) and Route 12 (Right), visual system and offset combinations are evaluated relative to visual resolution (increasing from top to bottom). Conventions as in Figure 5.5.



Figure 5.7: **Evaluating aliasing.** To investigate the potential for aliasing we ask which of the training views from along the route matches best for each eye when at the test locations. The Alias score is derived from the position of the best matching view in the training view sequence relative to the position of the correct training view. A: The mean aliasing per Field of View over all test locations decreases with increased Field of View and this effect is more pronounced for lower resolutions. We insert the dotted lines just for visualisation of the decreasing aliasing effect with increasing FoV. B: For each resolution we look at how aliasing varies as a function of displacement from the training route. Plots show the mean for each resolution and all FoVs with coloured area representing the standard error.

Using different routes results in very similar successful visual system combinations (figure 5.6).

5.3.3 Aliasing

Aliasing occurs for all tested resolutions and FoVs, but less so for higher resolutions and larger FoVs (figure 5.7A). Also, it increases with increased distance to the original route (figure 5.7B). Considering the sum of all performances for all FoVs and Offsets, this reduces the overall performance to 94% compared to the perfect memory performance. Results for Route 3.

5.4 Discussion

5.4.1 Takehome message

Steering in insects is achieved by an imbalance of activity between left and right descending neurons towards the motor centre. As sensory computation pathways are hemispherically divided, we investigated, how two Fields of View instead of a single panoramic Field of View can aid in Snapshot Navigation. Inspired by the imbalanced hemispheric activity within the LAL leading to a steering response, we explored how a difference in familiarity between a left and right Field of View could achieve a steering response towards the goal direction. We found that by subtracting the familiarity values from one hemisphere from those from the contralateral hemisphere generates at least 75% 'correct' steering responses towards the goal-direction from off-route locations within $\pm 90^{\circ}$ of the route direction, given large Field of Views and medium to large Offsets. This performance increases with reduced visual resolution and is only slightly negatively affected by aliasing. Therefore, we have shown the plausibility of a steering mechanism based on the inter-hemispheric difference in image familiarity for Snapshot Navigation.

5.4.2 Building on pixel-by-pixel comparison

For processing of the images we used pixel-by-pixel comparison, as this stage of processing isn't meant to be biologically plausible, which made the familiarity processing a simple mathematical operation. This approach can lead to several hurdles though, especially in dynamically changing environments, for example, the same location's raw value visual representation changes dramatically with different lighting. To compensate for this, several image processing methods have been proposed. While some methods revert back towards feature detection, as with skyline (Graham & Cheng, 2009), landmark (Möller et al., 1999) or Haar-like features (Baddeley et al., 2011), others take a holistic frequency filtering approach (Stone et al., 2018; Meyer et al., 2020). More computationally intensive methods like object recognition could be employed, too - most likely for simple shapes only though, as insect vision is rather low resolution. Regardless, as our approach can be seen as the bare-minimum to achieve a steering response, any additional 'cognitive' process therefore should increase the performance or make it more reliable with environmental changes.

Another filtering approach can be downsampling of the image size, which effectively acts as a low-pass filter, thereby cancelling out high-frequency noise, akin to the low resolution visual systems of insects (Stürzl & Mallot, 2006; Gerstmayr et al., 2008; Baddeley et al., 2011). Downsampling had a positive effect on the performance, as has been shown for visual place recognition before (Milford, 2013; Wystrach et al., 2016b).

The extent of how much and which type of visual information is transferred from the contralateral hemisphere is currently unknown (Habenstein et al., 2020; Li et al., 2020). Indicated by our best performing visual setups, the more visual information each memory can capture, the better the setup performs. This would mean, it could

be beneficial for some visual information to be transferred to the contralateral memory. However, a FoV covering only ipsilateral visual information can be successful too, if in combination with at least a medium Offset (for example FoV 90 %90 %). A previous investigation of multiple visual fields for Snapshot Navigation yielded increased performance with increasing number of visual fields, with two fields being the optimal trade-off between the number of fields and the computational effort of determining rIFFs (Wystrach et al., 2016a).

5.4.3 What to remember

While we mainly focused on investigating how the hemispheric familiarity difference mechanism works with the 'correct' memory, the matching process in an autonomous agent may be less accurate. Because the agent does not know its location but only the snapshots, and possibly every snapshot has to be considered. Thus, aliasing can occur, where the most similar snapshot actually originates from another location along the route (Knight et al., 2020). Aliasing typically reduces performance. Additionally, comparing each query image to all snapshots can become computationally expensive, as this method scales linearly with the snapshot number.

An attempt to reduce aliasing is inspired by ants' apparent sequential memory, where they expect certain views to occur after another (Schwarz et al., 2020). Algorithmically, a temporal window can be introduced, where only a limited amount of the sequentially stored snapshots is used for familiarity detection. This way, general aliasing can be minimised as well as more complex routes followed (Kagioulis et al., 2021).

Other organisations of memory have been proposed in contrast to the standard procedure. One could be the distinction between attractive and repulsive memories, where the agent would not only take snapshots of the direction to move towards (attractive, towards the goal), but also of the direction not to move towards (repulsive, 180° away from the goal, Le Möel & Wystrach (2020)). This process resulted in a fine scale sinusoidal movement trajectory (undulations). While we used an attractive memory, an additional repulsive memory could emphasize a steering response with the attractive memory pulling towards the goal-direction and the repulsive memory pushing away from the anti-goal-direction.

Yet another different approach ties the panoramic memories with steering instructions. Whenever the heading direction is off towards one side of the goal direction, steering towards the goal direction the memory gets tagged with that steering direction, where the steering instruction could originate in the LAL (Wystrach et al., 2020b). Part of their modelling revealed that route following became more robust when the snapshots were stored with an Offset.

We, too, found an Offset to increase our model's success of steering towards the route direction when rotated away to either side. This could indicate that snapshots may not be captured when an agent's heading is aligning with the route direction, but when the agent's heading is at an angle in relation to the route direction. Many ant species undulate along the route they are following (Graham & Collett, 2002) which could be part of the strategy of storing the snapshots with an Offset. Undulation results with either eye facing more of the route direction than the other for a time, during which the familiarity of the route facing eye would be higher than the other. With the angles, which we call Offset, the biggest differences between the hemispheres occur around those (figure 5.5C), which would result in a stronger steering response back towards route direction. Undulations could be a result of a hemispheric difference steering mechanism, as it would bounce forth and back between leftward and right-ward steering. Since the observed undulations in ants are rather regular however, this could also mean that a source of the undulations may be an internal undulation generating mechanism structure, such as the LAL. Such a mechanism also may be



influenced by other modalities, such as optic flow (Pansopha et al., 2014).

Figure 5.8: **How familiarity difference relates to underlying trajectory shape.** Left: An agent is set to follow a sinusoidal movement trajectory (blue) after being trained with the views from along an underlying route (red). Right: for the cutout section (orange) of sinusoidal trajectory we show (upper) the orientation change d° of the agent and (lower) the would be steering response which is driven by the familiarity difference (dLR). The shaded regions in the lower panel represent points at which the derived steering response is 'correct', where headings towards the left of the route would initiate right-ward steering responses and headings towards the right of the route would initiate leftward steering responses.

Overlaying an undulating trajectory to route following while applying our steering mechanism shows that the would-be steering responses for off-route locations and off-heading rotations can result in the correct steering responses (figure 5.8). Applying this strategy to routes will be part of future work.

5.4.4 Integration with other insect brain models for navigation

As this investigation is purely algorithmic, a possible integration of this hemispheric imbalance principle could be by adjusting other brain inspired algorithms for the indi-

vidual stages of our method. As many models tackle specific questions and mechanisms in isolation, using them in concert would force the adaptation to proceed in a reciprocal manner, where the interaction dictates each models assumptions to become specific. This way, knowledge gaps can be better identified and narrowed down, or individual model assumptions improved and corrected.

The visual memory could be stored using a MB inspired neural network (Ardin et al., 2016), investigating how two set up two independent hemispheric memories and how visual information can be transferred to the contralateral side. The Offset could be achieved by using a CX model (Stone et al., 2017), as those models deal with spatial perception. The CX also is used for PI (Stone et al., 2017) and deals with additional modes of navigation (Sun et al., 2020). Therefore it would be interesting to focus on how visual place recognition, which does not actively consider the relationship between the global position of the agent and the subjective position estimation, interacts with a modality, which does. Steering finally can be achieved by feeding the CX output into a LAL model, which additionally generates small scale search behaviours dependent on the reliability (here: familiarity) in order to pursue navigational stimuli (see chapter 6 and Appendix). An active sensing behaviour adds a dynamic component to this mode of navigation, with the purpose of overcoming unfamiliar views by actively searching for familiar views. This innate movement activity then would put the other navigation models to the test, how these perform with a more realistic embodiment.

5.4.5 Conclusions

Snapshot Navigation has long been investigated with a panoramic scene in mind. This approach works well in many scenarios, however, while ants treat scenes panoramically under certain aspects, this approach does not capture the whole picture. Recent studies suggest, that each ant eye's view matters on its own. Both disabling the view of one eye affects the navigational capabilities (Bühlmann, unpublished data) as well as disabling the memory substrate (MB) of one hemisphere does (Buehlmann et al., 2020). As our study suggests a familiarity relationship between both hemispheres could be used to recover the goal direction. Based on the range of visual input availability to each hemisphere's visual memory, both using only ipsilateral visual inputs as well as using contralateral visual inputs enable this orientation recovery mechanism. We hope that the idea of hemispheric imbalance will spark similar kinds of modelling attempts within Snapshot Navigation especially, but also further behavioural and neurophysiological experiments.

Further investigations may focus on identifying, under which circumstances this mechanism succeeds or fails - a more detailed analysis of how visual memories and queries relate to each other. This could lead to eventually add other pre-processing steps other than mere cross-correlation to calculate visual familiarity. Maturing this mechanism may enable future autonomous agents to use a reliable but low-processing visual compass, which has been designed with a dynamic movement and dynamic environment in mind.

6 Chapter 5: A bio-inspired snapshot algorithm using active sensing

This chapter was written and the experiments designed and executed by FS. PG supported with the experimental designs and editing. EK and AD helped with setting up the Antworld pipeline.

This chapter uses the Core SNN model from chapter 4 with realistic, complex sensory stimuli. This is an extension of previous work on a simpler version of this experiment. This was accepted after peer review for the Living Machines Conference and the paper can be found in the Appendix.

Steinbeck, F., Graham, P., Nowotny, T. and Philippides, A., *Can Small Scale Search Behaviours Enhance Large-Scale Navigation?*, 2020, Living Machines 2020: Biomimetic and Biohybrid Systems, pp 338-341.

Abstract

Previous central place navigation algorithms using the snapshot method employed panoramic images and stereotypic movements. These work well when close to a memorised route or place, but are less capable of recovering when deviating too much. Here we introduce the usage of two visual Fields of View and adaptive movement control using an insect brain inspired Spiking Neural Network for a central place navigation task. We used a virtual environment for the generation of realistic visual inputs. Based on snapshots pointing towards a designated central bush, a grid around this central place was created by calculating the direction of highest familiarity. Virtual agents using different combinations of panoramic vision, bilateral vision and the Spiking Neural Network were deployed to follow the direction of highest familiarity of the closest grid point. We found that using two Fields of View vastly increases the successful navigation towards the central place in comparison to panoramic view. Adding adaptive movements improves the success in comparison to stereotypic movements even further. Taken together, both using bilateral vision instead of panoramic vision and using an adaptive movement control strategy improve success in this central place navigation task in this simulation.

6.1 Introduction

Successful navigation in a complex environment requires an agent to both recognise stimuli which aid in finding the correct direction and to move itself around in this environment. Many insect species using vision for navigation employ a snapshot type mechanism, where the subjective views of significant places are memorised. This is mostly thought to be applied when either remembering a central place (Tinbergen, 1938), like a hive, or when traversing a route from usually a food source to the hive (Collett et al., 1992).

Based on early work in bees (*Apis mellifera*, Cartwright & Collett (1983)), snapshot algorithms have been established to replicate this behaviour in an abstract way. Using panoramic vision, images taken in the vicinity of memorised snapshots can be compared to those snapshots and a difference score calculated (Zeil et al., 2003). The closer to the original snapshot location, the smaller the image difference, enabling gradient descend to the original snapshot location. Rotating the query images while comparing them to the snapshots, the heading direction of the snapshots can also be recovered (Labrosse, 2006). These mechanisms then can be applied in a stop-scan-step fashion, where the agent scans the entire panorama, creating a rotary image difference function (rIDF), comparing the query panoramic view to a snapshot into every direction. The minimum of the generated function indicates the direction to move towards (Baddeley et al., 2011; Wystrach et al., 2013; Le Möel & Wystrach, 2020).

While ants scan their environment occasionally, their typical movements resemble a sinusoidal trajectory (Graham & Collett, 2002) instead of constant pirouettes. Constant scanning exploits the visual information maximally at every step, which would result in not only high computational effort, but also slow movements in a real world scenario. Zig-Zagging on the other hand incorporates the scanning process as a more dynamical mechanism. Ants' Zig-Zagging trajectories become more curvaceous in unfamiliar locations, increasing the underlying scanning mechanism. This way, Zig-Zagging serves as a dynamically adapting active search mechanism for familiar stimuli.

Adaptive behaviours are realised with motor control, where the production of active movement strategies shapes the acquisition and usage of sensory information. Most motor systems utilise central pattern generators (CPGs), which are neural circuits that produce rhythmic outputs in the absence of rhythmic input. They have been found in the control of swimming movements of lamprey (Ijspeert, 2008) or movement control in invertebrates (Grillner et al., 1991). CPGs have also been shown to be useful components for motor control in bio-inspired robots (Selverston, 2010).

In insect brains, the Lateral Accessory Lobe is a pre-motor area that has been shown to generate CPG like outputs in certain conditions (Kanzaki et al., 1992; Mishima & Kanzaki, 1999; Iwano et al., 2010; Pansopha et al., 2014; Namiki et al., 2014). It is a conserved brain structure and is fundamental to a range of sensori-motor behaviours such as pheromone search in silkmoths (*Bombyx mori*, Kanzaki & Shibuya (1992)) and phonotaxis in crickets (*Gryllus bimaculatus*, Zorović & Hedwig (2013)). Computational models of the LAL have been developed to obtain a better understanding of how the LAL network can generate "flipflop" activity (Adden et al., 2020) or how the LAL may contribute to pheromone plume tracking (Chiba et al., 2010). Here, we address the two properties of biological plausible movement control and snapshot computation mechanisms. We apply our previously developed spiking neural network model, which is inspired by the steering framework based on the LAL (Steinbeck et al., 2020a). If the sensory familiarity is high, the agent steers towards the spatial origin of that percept, but if it is low, the agent starts moving with a stronger sinusoidal trajectory, which leads to a greater scanning of the environment. Given it is currently unclear, how the visual information is processed in order to achieve Snapshot Navigation we investigated the catchment area of a visual system using biologically plausible organisation of two visual fields (Wystrach et al., 2016b, 2020a). Instead of using one panoramic view, using the familiarity difference between two views enables a steering response towards the snapshot heading direction. Therefore here, we investigate how bilateral vision can be applied in a central place navigation paradigm, and additionally, how an Active sampling component can be applied to aid in Snapshot Navigation. We extend our previous work, where we investigated how a active sensing aids with approaching a single stimulus (see Appendix), by situating the models in a 3D-environment LiDAR scan of a real experimental test site (Risse et al., 2018).

6.2 Methods

Simulations and analyses were performed using Matlab (MathWorks, Natick, MA, USA) and Python.

Antworld Image Rendering The rendering pipeline was the same as in Chapter 5 Methods section, using the LiDAR scanned environment from a experimental test site in close to Seville, Spain (Risse et al., 2018). This data allows for the generation of close to naturalistic rendered images and navigation within the layout of a real environment. We chose a central place at the location of a shrub, between other

shrubs. From this central place, the Snapshots were placed at a distance d = [0.5, 1, 1.5] m radially every 60°, therefore 18 snapshots pointing towards central place (see figure 6.1). The grid extended into x & y by 4m with a 0.1m resolution. The rendering resolution at each point was 90*20 pixels.



Figure 6.1: A top-down view on the virtual environment "Antworld". The blue spots represent snapshot locations aimed at the centre of the grid. The red spots are the query grid locations, each of which is compared to the snapshots.

6.2.1 Familiarity grid

In order to compare navigation based on familiarity with panoramic vision (Cyclops) or bilateral vision, we calculated rotary Image Familiarity Functions (rIFFs) for both types of vision (for more details on the familiarity calculations and other peculiarities read the methods section of chapter 5). These rIFFs were calculated from comparing each grid image with all snapshots first, and then choosing the one with the highest produced familiarity. This procedure we repeated for both panoramic vision and bilateral vision, with both eyes covering a Field of View (FoV) of 90 %90° (frontal overlap/rear blindspot) and a memory Offset of 45°. The values of highest familiarity indicated the direction to ideally move into. At this point, the direction of highest familiarity is indicated by a

single value for panoramic vision; for bilateral vision, we calculated the mean direction between the left and right eye instead. Furthermore, we calculated the weighted mean direction between the eyes by weighting the mean from the values of highest familiarity each rIFF displays in the location. This idea we derived from the strength of familiarity determining the strength of steering, as it would be for our steering framework. These values of highest familiarity direction then were assigned to each grid point.

6.2.2 Central place navigation: perfect memory

First, we compared the effect of using panoramic vision (Cyclops) compared to bilateral vision (Braitenberg). While the Cyclops represents the previously established method for Snapshot Navigation, the Braitenberg represents an agent using lateralised sensory stimuli for steering - in this case, a direction of highest familiarity determined by two FoVs. In order to investigate how familiarity shapes the rIFF trajectories taken within this grid, we let simple agents perform navigation with perfect memory. Using the precalculated direction of highest familiarity, an agent is spawned at each grid point and instructed, to walk into the direction of highest familiarity of the closest grid point. Each agent ran for 500 repetitions and a step size of 0.1m. The procedure stayed the same between conditions, except for the input used, which was the directions of highest familiarity generated with panoramic vision or with bilateral vision.

6.2.3 Movement dynamics adapting to familiarity

Here we show, how familiarity can be used to dynamically adapt movement patterns using the Core-SNN from chapter 4. For this we assigned to each grid point the value of highest familiarity. In order to make the changes of values smoother, we interpolated the familiarity grid using MatLab's interp2 function with the "cubic" option, increasing resolution from 100mm to 5mm. We increased the difference of these values to fall between 0.25 - 1 familiarity (the original range lies between 0.78 - 0.93 familiarity). The familiarity value of the closest grid then is fed into the input neurons

of the Core-SNN. The behaviour chosen resembles the one shown in figure 5.5 B(a), where low familiarity input produces a relatively stronger Zig-Zagging trajectory than with high familiarity input. The only adjustment taken were the final distance and steering values, fitting them into the dimensions of the new environment.

6.2.4 Using bilateral familiarity and a SNN for steering

Here we investigated the interplay between an active steering component and active search component using the Core-SNN. In our Bilateral Vision for Snapshot Steering work (see chapter 5), we found the effect of calculating the difference of familiarity between left and right eye as a mechanism for the recovery of the original snapshot heading direction. Since we analysed this effect only quantitatively so far, here we hardcoded a steering component, if the agent faces \pm 90° as the direction of maximum familiarity of the closest grid point. This component is maximal if the direction of maximum familiarity and the heading direction align with familiarity being 100%, and decreases linearly within the \pm 90° range to the familiarity of 25%. If the agent faces outside of this range, it resorts to the small scale search behaviour, with the familiarity set to 25%.



Figure 6.2: **Familiarity changing movement dynamics using the SNN**. *Left column*: An Agent is instructed to use the value of highest familiarity of the closest grid point. Each grid point shows the value of highest familiarity. Top: Panoramic visual input familiarity, Bottom: bilateral visual input familiarity. *Right column*: Zoom-in showing the changing movement dynamic when exposed to changing familiarity.

Here we compare three conditions: 1. the Core-SNN using the original panoramic rIFF as a Cyclops, 2. a Braitenberg-SNN (which is the Core-SNN with the CPG component disabled) using the just described steering instructions and 3. the Core-SNN using the just described steering instructions (BBCPG).
$A \xrightarrow{R} \xrightarrow{L} \xrightarrow{0^{\circ}} \xrightarrow{0^{\circ}$

Figure 6.3: **Steering convention.** *A*: (Left) Hypothetical rIFFs for a left(blue) and right(yellow) eye in one position, (Centre): the same rIFFs radially pointing into 2D-space, (Right): The mean angle between the two most familiar angles (left), or the weighted mean angle between the most familiar angles with different strengths (right). [R = Direction of highest familiarity right, L = left, M = mean angle, WM = weighted mean angle] *B*: The visual organisation for the perfect memory walk: Cyclops, Braitenberg & Weighted Braitenberg. *C*: The visual organisation and input into the SNNs for the SNN walk: Cyclops, Braitenberg & BBCPG, with the same neuron colour codes as in figure 4.2.

6.2.5 Statistics

We measured the performance of the navigation experiments by analysing the trajectory length, final endpoint distance from the central place and the percentage of all agent simulations reaching the vicinity of the central place. To the lengths and endpoint distance we applied a Kruskal-Wallis (KW) test, which is used to determine whether or not there is a statistically significant difference between the medians of three or more independent groups. The Kruskal-Wallis test does not assume normality in the data. Finally we used the Multcompare function of MatLab, which performs a multiple comparison of the group means (Post-Hoc test, PH). A χ^2 test was performed to assess the relationship between the group percentages of agents reaching the central place.

6.3 Results

Perfect memory rIFF walk First we wanted to explore the difference between using panoramic vision compared to bilateral vision in the context of central place Snapshot Navigation. By following the directions of highest familiarity from each grid point we can estimate how an agent would approach the central place using this information only. Baseline was the established scan-step type of navigation using panoramic vision - the change of behaviour by using a differently organised visual input was quite stark (figure 6.4 left column).

The Cyclops tended to converge to the closest vegetation (figure 6.4 A). In more "open" places, the rIFF was more correct for guiding towards the central place, but other vegetation blocking the view to the central place seemed to attract it away (figure 6.4 E). Therefore, the median distance travelled (0.6m), the median final position from the central place (3.22m), the amount of paths leading to the central place (11%) and the median distances travelled leading to the central place (0.8m) were comparably less successful than the bilateral versions.

The most obvious difference to the Cyclops was the establishment of routes when using bilateral vision (figure 6.4 B & C). These routes seemed to trace through rather open spaces not towards the vegetation itself. Most routes lead towards the central place (41%), resulting in \sim 375% more agents reaching it compared to the Cyclops(11%). Overall, most agents did not converge on nearby vegetation but travel further distances, creating these routes. The difference between computing the direction of highest familiarity using just the mean direction between the eyes or the weighted mean, was negligible.

Overall, the reorganisation of the visual inputs from one panoramic FoV to two FoVs

has improved the navigational success of finding a central place with Snapshot Navigation.



Figure 6.4: **Central place navigation with conventional rIFF movement strategy.** A-C: An Agent is released in each grid point (seen as in figure 6.1), instructed to follow the direction of highest familiarity of the closest grid point. Each grid point shows the (average) direction of highest familiarity. A: Panoramic visual input, B: Average bilateral input, C: Weighted by strongest familiarity average bilateral input. D: The distance travelled [m] shown as violin plot, where the width shows the distribution by distance; KW revealed no significant differences ($\chi^2 = 6.92 \cdot 10^3$, p = 0, df = 2) among the three categories, PH revealed no significant differences ($\chi^2 = 207$, p ≈ 0 , df = 2) among the three categories, PH revealed no significant difference between B & BB with p = 0.82. F: Of the percentages of reaching the target area, there was only a significant relationship between the groups Braitenberg & Weighted Braitenberg with χ^2 (df = 2, p = 0.75). G: The median distance travelled by winners [m] with errorbars showing standard deviation,KW revealed no significant differences ($\chi^2 = 1.192 \cdot 10^3$, p ≈ 0 , df = 2) among the three categories. PH revealed no significant difference between B & BB with p = 0.82. F: of the percentages of reaching the target area, there was only a significant relationship between the groups Braitenberg & Weighted Braitenberg with χ^2 (df = 2, p = 0.75). G: The median distance travelled by winners [m] with errorbars showing standard deviation,KW revealed no significant differences ($\chi^2 = 1.192 \cdot 10^3$, p ≈ 0 , df = 2) among the three categories, PH revealed all results to be significantly different. *s are shown for p ≤ 0.001 on PH comparisons.

SNN walk This was an investigation of introducing a bio-inspired movement algorithm in place of the scan-step method, while additionally adding the difference between left and right eye familiarity effect for steering (based on chapter 5). Both the dynamic behavioural component from the Core-SNN, as well as the steering component benefited the overall success of navigating towards the central place.

Using the SNN, the Cyclops reached the central place the least frequently (17%) compared to the steering variants, but more often than without the SNN (11%). The overall activity around vegetation was higher than the open spaces, as indicated by darker areas in the trajectory plot (figure 6.5 A).

The Braitenberg SNN performed similarly (40%) as the perfect memory Braitenberg (41%), whereas the BBCP (46%) outperformed even the Braitenberg. The Braitenberg and BBCPG followed the same routes as with the perfect memory (figure 6.5 B & C). The BBCPG covered overall more surface than the Braitenberg due to its CPG component, making the paths look more blurry; yet, the distance travelled overall decreased with the BBCPG (figure 6.5 A).

Conversely, the median distance travelled by the successful agents increases from Cyclops (1.9m) over Braitenberg (2.9m) to BBCPG (3.5m, figure 6.5 G). Using the



SNN had the effect, that the agents either found the centre or mostly missed it altogether (figure 6.4 E), compared to not using the SNN (figure 6.4 E). Figure 6.5: **Familiarity guided steering with the SNN.** A-C: An Agent is released in each grid point, instructed to steer towards the direction of highest familiarity of the closest grid point using the SNN. Each grid point shows the (average) direction of highest familiarity. A: Panoramic visual familiarity guiding the SNN, B: Average bilateral familiarity guiding a Braitenberg SNN, C: Average bilateral input using a the SNN. D: The distance travelled [m] shown as violin plot, where the width shows the distribution by distance; KW revealed no significant differences ($\chi^2 = 908$, p ≈ 0 , df = 2) among the three categories, PH revealed all groups to be significantly different. E: Final distance from centre [m], KW revealed no significantly different. F: Of the percentages of reaching the target area, there was no significant relationship between all groups. G: The median distance travelled by winners [m] with errorbars showing standard deviation,KW revealed no significant differences ($\chi^2 = 627$, p ≈ 0 , df = 2) among the three categories, PH revealed all results to be significantly different. *s are shown for p ≤ 0.001 on PH comparisons.

Also the replacement of a rigid scanning procedure with a dynamic and adaptable active search algorithm has improved the navigational success of finding a central place with Snapshot Navigation.

6.4 Discussion

We investigated how an active sensing mechanism alongside bilateral vision can aid view based navigation. We found that a reorganised visual input into two Fields of View with a memory Offset increases the success rate of navigating towards a central place. Furthermore, adding an active sensing component increases the navigational success rate.

6.4.1 It's about the eyes

How does the organisation of the visual inputs matter for a mechanism which uses the input holistically? Panoramic vision enables a holistic view of the environment and therefore should enable the maximum use of information for Snapshot Navigation. The more visual information is available, the easier it is to memorise the uniqueness of a scene. However, that information is all connected to the single view tied to a single orientation. Dividing the entire panorama into sub-fields may be beneficial for familiarity Snapshot Navigation as with an increased number of fields performance can increase (Wystrach et al., 2016a). Several further possibilities may lead to the stark difference of behaviour between a single panoramic view and multiple FoVs in our tests. One could simply be the increased number of chances to catch a correct view. Furthermore, with the 90 %90 ° FoV several effects could be leveraged. Using oversampling where parts of the views overlap, could lead to an increased chance of detecting the same patterns with each eye. This effect could be increased by the rear blindspots, as some parts of the scene will not be part of any memory, therefore reducing the chances of recognising parts of the scene, which would not lead into the correct direction anyway.

Based on our visual field exploration in chapter 5, we chose a conservative combination of Field of View and Offset with bilateral agent's steering based on the integration of two recovered directions. This reliably lead to a comparable performance versus using strict rIFF navigation, where the agent would turn on the spot to determine the most familiar direction. This adds to the evidence that using multiple Offset memories can increase navigational success (Wystrach et al., 2020a). An Offset memory could indicate the circumstance a snapshot was taken in, which could happen when the agent is not aligning its body axis with the target direction, but periodically off-target, when one or the other eye has more of the goal-direction scene in its FoV. Therefore, two memories could be created for each eye independently. When the query image and snapshot then align, the steering instruction would be strongest into the direction away from the eye-side, as in if the left eye recognises a familiar scene, steer to the right. This could explain partially why ants display Zig-Zagging trajectories.

6.4.2 Moving onwards

Most snapshot algorithms so far have used static movement instructions, which do not adapt to a change of the view familiarity and therefore its reliability. While this type of movement works well in close vicinity to a snapshot location or route, once the agent is lost, finding back to locations with familiar views is up to chance. Also, returning to the route is near impossible, as agents tend to stay on trajectories parallel to the route.

Here, the agents use the familiarity as a reliability score to directly modulate movements. Even when the familiarity is weak, an agent keeps on moving, whereby it can avoid getting stuck at non-familiar locations. Furthermore, due to the increased variability of movement patterns in unfamiliar places, the agents can increase their chance to move towards a neighbouring location with a vastly different rIFF, which may or may not lead towards the goal. This component, as introduced with the CPG, seems to be more beneficial than detrimental, as the number of successful agents increases by at least 12% between using the bilateral familiarity information without and with the CPG. Here we say at least, since we used a conservative Zig-Zagging behaviour. Using another type of search behaviour could increase the number of successful agents even further.

A similar approach using a familiarity dependent sinusoidal trajectory generation had been applied on a robot before, successfully following a route (Kodzhabashev & Mangan, 2015). This setup very much resembles our Cyclops-SNN agents, which also use a panoramic view to modulate Zig-Zagging trajectories.

Using movements to improve sensing capabilities is a common theme in nature and robotics. Many of these movements are restricted to moving the body parts, such as saccades with eyes (Juusola et al., 2017; Land & Nilsson, 2002) or whisking for haptic exploration (Mitchinson et al., 2011; Grant et al., 2014). Others even use whole body movements to trace the source of relevant stimuli (Iwano et al., 2010; Wystrach et al., 2016a; Lent et al., 2010). In robotics, active perception is an emerging field, often using machine learning techniques to identify an effective active movement strategy for shaping stimulus collection (Bajcsy, 1988; Queralta et al., 2020).

6.4.3 Future endeavours

Since here we hard-coded the steering instructions, in the future, a more in-depth analysis of the difference between left and right familiarity values is needed. So far, we analysed the resulting correct steering responses only quantitatively. As can be seen at the bottom of figure 5.2, the difference values can vary vastly. Therefore, these values may be filtered in order to result in a sensible steering response.

Another route of inquiry would be to design behavioural experiments in ants that focus intensely on the low level movement dynamics. The individual routes generated here can be used as a reference for tracked movements in naturalistic environments or simulated environments.

Previous experiments tracing ants in a natural environment mostly focus on the highlevel movement trajectories. While some of these have produced snippets of this line of research, the generated data would not be merely enough to being able to make qualitative analyses (Mangan & Webb, 2012; Collett et al., 2013; Schwarz et al., 2020). Therefore, a possible experimental method could be the use of a highresolution camera on a gantry which is placed over the experimental route location. This would increase the range of trackable movements and depending on the resolution, making the low level movements visible.

Alternatively, recent advances in computational devices have made virtual reality setups more achievable. Therefore, ants could be trained in this the "antworld" virtual environment, using a virtual reality setup designed for ants (Goulard et al., 2020; Kócsi et al., 2020). This would make low level movement dynamics easiest to track, as the ant will only move in the very controlled setup.

On the movement side, the dynamic component is closely related to the environment dimensions. Therefore, the movement- and steering-speed could be better adjusted

to this environment. Furthermore, stronger sinusoidal patterns or other behavioural search dynamics, as seen in figure 4.4, could be tested to investigate which type works best in this scenario or others.

Ultimately, we want to determine a good trade-off between the visual familiarity calculation effort and the Active sampling effort. How much does an agent need to move to be able to find the most familiar direction? How can the familiarity difference between two eyes be used most efficiently? Understanding that relationship could be very interesting for future view based navigation systems.

7 Chapter 6: Conclusions

This thesis touches a wide range of disciplines and therefore this last chapter is intended to reiterate the most important implications of the research. More specifically I will consider seperately the implications from abiological and then an engineering perspective.

7.1 Impact on Biology and Insect-Neuroscience

Using computational modelling in Biology dares the "What if...?". Combining the knowledge about neurophysiological mechanisms and observed behaviours, the knowledge gaps are attempted to be filled by making assumptions about unknown parameters, to best approximate the observed behaviours. The basis for the modelling in this thesis is introduced in chapter 3 with a steering framework based on insect behaviour, -anatomy and -physiology of the Lateral Accessory Lobes LAL. The LAL is a conserved brain area found in all insects (Thoen et al., 2017) and is dubbed the pre-motor region (Namiki et al., 2014). This then is converted into a functioning spiking neural network in chapter 4. Building on this framework, we investigate how a visual familiarity mechanism using two visual fields can be integrated to the steering framework, chapter 5. Combining those two modelling ideas, in the last chapter 6 the SNN and bilateral familiarity ideas are integrated with each other to be applied in a central place navigation task in a realistic modelling environment.

Capturing the many necessary variables to explain certain biological mechanisms can be especially time consuming, if not impossible, with current technologies. Therefore, in the process of computational modelling, particular mechanisms are attempted to be explained with less complexity than in reality, with decisions made about which less impactful variables to omit. This can be achieved by exploring the extreme cases and in non-realistic contexts, breaking them down to their core components. While pure experimental Biologists or Neuroscientists often chase down ever more detailed information in their organism, they may loose track of the context. This is where modelling work, like that attempted here, comes in. And we can then ask: How can we fit different mechanisms together? What are the commonalities between similar mechanisms? And, what assumptions do we need to take to build a functioning model? Taking it to the final stage, these models then can be applied on robotic platforms, exposing them to real-world scenarios and testing their validity (Webb, 2020). Within our modelling attempts we reduced complexity in the SNN work mostly to a

conventional Hodgkin-Huxley approximation, modelling the typical electrical currents occurring in common neurons. And similarly, while the output of the LAL SNN model was designated to generate movements, this conversion was focused on how firing rate might relate to force generated by muscles, but no additional physics such as friction or inertia was considered.

In the bilateral snapshot work, although we used a realistic simulation of the natural foraging habitat of a desert ant, we did make some simplifications. The movements were not adapted to the terrain of antworld, which was not perfectly flat. Furthermore, the virtual environment did not include any lighting-condition variations, which may be important to make the simulation more realistic.

Despite these simplifications, we believe that the modelling work was pitched at a level that has important implications for our understanding of the function of the insect brain structure LAL, how it may be involved in the generation of small scale search behaviours and how its hemispheric organisation may have implications for sensory input computations. We discuss these specific points further below.

7.1.1 The generation of small scale search behaviours

Small scale search behaviours, also called active sensing or exploratory movements can be observed in all moving life forms. An unlikely example is the exploratory growth of plants, such as climbing vines or how common field peas grow so that their tendrils

can find solid structures to attach to and use those to grow upwards more quickly (Darwin, 1880; Gallentine et al., 2020). Equally remarkably, single celled slime molds grow initially into all directions for exploration to find food sources in their immediate surroundings (Tero et al., 2010). Humans also rely very much on active sensing movements to improve their perception, such as saccades or veering (Land & Nilsson, 2002). All of those are employed to increase sampling of the immediate environment to aid navigation towards a particular goal. Insects are no exception, as they also employ small scale search behaviours. A common theme in many insect species across sensory modalities are types of Zig-Zagging behaviours. These are seemingly very effective, as these are employed so very often.

One of the major outputs of this Thesis is to propose a possible neuronal brain mechanism for the generation of small scale search behaviours in insects(see figures 3.2, 3.4, 3.5), which is inspired by the connectivity and behaviours of the LAL (see figure 3.2). As this is a conserved brain structure among all insect species, the LAL is an ideal candidate for being involved in the generation of many of the just mentioned observed Zig-Zagging with its easy adaptability to generate reliable search dynamics.

The circuits I have proposed is inspired bydirect, physiological (Kanzaki et al., 1992; Mishima & Kanzaki, 1999; Iwano et al., 2010; Zorović & Hedwig, 2013; Namiki et al., 2014; Bidaye et al., 2020; Rayshubskiy et al., 2020) and circumstantial, behavioural (Goodman et al., 1987; Ibbotson & Goodman, 1990; Pansopha et al., 2014; Martin et al., 2015) evidence. Due to the LAL's presence in all insect species, I was able to compile findings into one, generalisable model.. Computational modelling and the consequent exploration of parameter space when setting up this model have shown that many different dynamic exploratory movements can be achieved. Coincidentally or not, these resemble movements observed in nature. Furthermore, with these many different parameter combinations leading to the typical Zig-Zagging behaviour, even when exposed to more computational noise, speaks of a robust network design.

The central aspect of this computational model is a CPG. CPGs are popular models explaining a wide range of neuronal dynamics, especially in motor control (for example controlling the contractions for a leg to produce movement, Ijspeert (2008); Mantziaris et al. (2020)). Here, this concept is elevated to a pre-motor control level, with a CPG controlling higher-level movement direction. Within our model ,the CPG and the sensory computing areas are directly linked. While in reality there are several computational levels between sensory apparatus and pre-motor regions, we just focused on visual memory as a computational mechanism and therefore. As this is a big abstraction of the computational pathways, we dubbed this a sensory driven CPG.

This underlying computational principle could shed a light on the periodically alternating steering behaviours observed in many insects, as these are often analysed from an external point of view. Assuming a certain Zig-Zagging frequency and therefore underlying Flip-Flopping frequency, our model parameters could be tuned to these observed parameters. While probably not being able to capture the observed behaviour as whole, it may lay a good foundation to model a range of small scale search behaviours across insect species and sensory modalities. An example for an application could be the learning- and homing-flights of wasps. Both behaviours display a type of Zig-Zagging, but with different underlying dynamics (Stürzl et al., 2016). Other modalities also utilise Zig-Zagging behaviours, such as pheromone plume tracking in the silkmoth (Kanzaki et al., 1992; Iwano et al., 2010). Furthermore, many ants have been observed to walk Zig-Zagging, when visually navigating. Tuning our model to those dynamics could give a better understanding about howexternal stimuli lead to the observed behaviour by providing a model of the internal dynamics and their interaction with sensory information.

Going beyond plausible accounts of how LAL might interact with sensory information to create diverse behaviours, it would be important to provide direct experimental proof of the role of LAL. One way to do this would be to discount the possible involvement of other neural circuits being responsible. Genetic tools in flis, and some other insects, would allow specific neurons, e.g. the LAL inhibitory neurons within the LAL, to be disabled and observations made on whether the agent still behaves in an unaltered way.

7.1.2 Using two eyes for heading recovery in visual navigation

How much abstraction is too much abstraction? Using panoramic images in insect inspired models of snapshot navigation was based on the very wide-field visual perception in Hymenoptera, but abstracted to a single hypothetical panoramic sensor. While using single 'monocular' panoramic images works reliably to follow routes (Baddeley et al., 2012; Ardin et al., 2016; Le Möel & Wystrach, 2020) for example, this may not reflect the computational principles used in the insect brain. Insect physiology is lateralised, where the body is mirror symmetric to the centre line. Insects posses a left and right eye, have a left and right brain hemisphere (Paulk et al., 2015) and a left and right motor centre. Also the LAL is divided into a left and right lobes, appearing to be wired mirror-symmetrically 3.2. The upstream lying MBs also are organised in two lobes, and they are the likely site of visual memories. This begs the question, can a visual familiarity signal for navigation can be lateralised, so that it may be used in a Braitenberg-like fashion for steering.

The basic idea was to investigate if there is a difference of familiarity between both eyes. This we did literally, by subtracting the familiarity value of one eye from the other eye's value. We then assigned the resulting value sign to either indicate a left- or rightturn. Calculating this for the entire panorama, we analysed how often the indicated turning direction resulted in the correct turning direction, leading back to the desired heading direction. This procedure we repeated for a variety of different FoVs for each eye, for different resolutions and different Offsets in order to investigate, if any visual receptor changes would result in changing, or improved, familiarity differences.

We found that using a bigger FoV and Offset resulted most reliably in the correct turning direction. This means, instead of having to scan the entire panorama, using this method can point towards the desired heading direction with a single operation. As this mechanism is part of dynamic behaviour, it could also result in a Zig-Zagging behaviour, where the agent heading would bounce between the directions of highest familiarity of each eye.

One implication of these findings is that a full single panoramic view is not necessary to successfully follow a route visually. Furthermore, the difference between the lateralised views seems to leverage in a way gradient descent signal, which is contained in the rotary Image Familiarity Function. By viewing the panorama in two directions simultaneously, the gradient may be calculated. This makes rigorous systemmatic scanning unnecessary on the one hand, while making the whole algorithm more robust to similar looking places.

This results in interesting questions for biological experiments: if the memories are used in a lateralised way, how do they interact with each other? Will disabling vision of one side result in the ability to visually navigate break down? How does it affect the mechanism at different stages during learning and recollection? Can this also be induced by manipulating the memory substrate?

In the recent years, experiments have shown how manipulating visual information to both the eyes or the visual memory brain areas affects visual navigation (Buehlmann et al., 2020). This indicates that a visual snapshot mechanism indeed may rely on the bilateral hemispheric organisation. How much of the visual information is communicated between the hemispheres is currently unclear (Li et al., 2020). But with our experiments we show, that while visual information from both eyes available to each

memory increases the success of the bilateral snapshot mechanism, it is not crucial for it. Yet, having two independent memories seems to be advantageous.

Therefore, we need to do the following experiments. On the physiological side, it would be useful to find a way to disrupt the communication between the left and right MBs. If the ants still would navigate unaffectedly, this mechanism would be completely independent in each hemisphere. If the opposite happens, this would indicate that the connection between the hemispheres is crucial for snapshot navigation. And if there was a way to make this disruption one directional (i.e. the left visual can be transferred to the right memory, but not vice versa), this effect could be investigated to a much more detailed degree.

On the behavioural side it would be interesting to see how ants specifically behave on routes, on which to one side the visual scene is rather sparse, and the opposite side visually rich. As our network would predict in its raw form a biased signal towards the richer side, studying how ants behave in such a context would be very insightful (Graham & Collett, 2002). Some parts of this experiment could be to switch the visual stimuli with each other, for example using card board stimuli next to the route, and then replacing them between trials to make one or the other side more visually recognizable.

7.1.3 Considerations of the Spiking Neural Network Models

Modelling the dynamics of the LAL could have been achieved with rate-based models. However, modelling these dynamics with the more complex SNNs lets us not only determine which parameters are important to a greater depth of detail, but also will allow for future modelling using experimentally derived neuronal parameters in the future. This deeper characterisation of spiking neurons allows also for more versatile "roles" to be assigned to individual units in a model. This can lead to models capturing far more biological detail as we have attempted with the comprehensive model and as we hope future modellers will continue.

The comprehensive model's main properties, beyond the core model, are the distinct steering vs propulsion strength neurons, and the split CPG neurons. While the distinct steering/propulsion property is based on already published works (Cande et al., 2018), the split CPG has not yet been shown. To better understand this potential CPG split, Type I or II neurons identified in the silkmoth would have to be silenced in a physiological experiment. In particular disrupting the ascending Type II neuron activity should result in the loss of CPG dynamics and therefore no Flip-Flop activity. Furthermore, if this were the case, we could find different populations of adapting neurons, which may be selected to achieve different Flip-Flop dynamics, depending on the behavioural goal. Also, testing the novel idea of Type I neurons creating Ackermann-steering may be achieved if the axon terminals to the contralateral LAL were silenced. This would also lead to insects not being able to rotate. Therefore, as all good models should, we have testable predictions that can drive physiological experiments.

As our SNNs are based on our generalised steering framework, the actual LAL networks in different insect species may look all different to this boilerplate meta-model. As shown in CX research, networks may differ depending on behavioural context and ancestral lineages (Pisokas et al., 2020). Therefore, mapping out the LAL networks in different model species such as silkmoths, crickets and fruit flies or even ants would give us deeper insights. Firstly, how different can these networks look, how are they adapted to ecology. And secondly, how big those differences need to be, to achieve a different functionality, when investigating the neurons' contributions to observed behaviours.

7.2 Impact on Engineering and Robotics

The main goal of this work was the improvement of our biological understanding of the functions and mechanisms within the LAL. Our approach was the development of computational models. Thereby we indirectly developed algorithms which can be used in other platforms such as robots. While these algorithms certainly would have to be adapted to specific use cases, the foundation of biologically inspired navigation algorithms has been laid.

7.2.1 An adaptive active search mechanism

Many navigation algorithms have a high level of planning and therefore accuracy, when they are fed with the desired sensory inputs. This methodology uses a lot of processing power though, and may not be applicable in dynamic situations. Therefore these algorithms still show shortcomings to most natural environments, when they lose the desired percept, such as a tracked sight to occlusion or the tracked sight looking to similar to other sights in the vicinity. A simple, but effective adaptive search mechanism, as developed here could be a (cost-)effective solution to improve or overcome this non-adaptive limitation in terms of stimulus perception. Instead of having a high-level, planned search effort, increasing sampling by physically moving the body in a Zig-Zagging manner may be all that is needed to achieve a greater perception reliability.

As an active search algorithm involves much movement, a use-case could be in lightweight robotics or soft-robotics, which are designed to interact with the environment in an active manner. Instead of high level planning, physical interactions are integral to their functioning. While they are harder to control due to their dynamic material properties (Polygerinos et al., 2017), this can even be taken into consideration with some of the computations can even be outsourced to the material properties themselves

(Paul, 2006). Active movements therefore would fit well into those dynamic systems, both to improve perception of internal and external stimuli.

7.2.2 An effective visual compass

The bilateral snapshot navigation algorithm has shown a great capacity for the recovery of original heading directions. Due to the algorithm using low-frequency signals, it may be an effective strategy to use it in a variety of visually distinct environments. Furthermore the algorithm uses simple mathematical operations on small images, making it energetically cheap. These two characteristics alone make it an asset to any visual navigation algorithm. It could be used to aid more high-effort navigation algorithms as an additional compass system, or as a key mechanism for teach-andrepeat navigation algorithms.

A possible use-case could be the integration of this snapshot algorithm with an opticflow algorithm to interact more dynamically with changing environments. Using the visual compass, an agent would be able to set overall target directions and the optic flow module could then provide a reactive component to either avoid other agents or to circumvent other unexpected obstacles such as objects in the environment which have changed and are not part of the memory.

7.2.3 Computational Neuroethology

Our modelling attempts consider how the brain, body and the environment interact with each other in the production of natural behaviour. In this context mechanisms regarding active learning, active sampling and behaviour focussed on the interpretation of neural circuits or algorithms are integrated. Therefore, computational models emerging from this line of research are especially well designated for robot applications, as embodied cognition is embedded in their origin.

7.3 Summary

Biomimetic projects like this often bring together many interdisciplinary fields of study. A major component is the synthesis of loosely connected pieces of knowledge. As pointed out here, both biological mechanisms may be better understood by attempting to build models which can interact with real environments, while engineering can leverage already successfully working mechanisms to overcome complex problems.

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8 Appendix



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 welldescribed 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 sensorydriven 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

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(Muller and Wehner, 1988; Wehner and Räber, 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

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 byproduct 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 moths' 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, medua; 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 (Pansopha 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 Strausfield, 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

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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) Pheromonetracking 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 zigzag 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 pheromonetracking 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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Can Small Scale Search Behaviours Enhance Large-Scale Navigation?

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Abstract. We develop a spiking neural network model of an insectinspired CPG which is used to underpin steering behaviour for a Braitenberg-like vehicle. We show that small scale search behaviour, produced by the CPG, improves navigation by recovering useful sensory signals.

Keywords: CPG \cdot Braitenberg \cdot Navigation

1 Introduction

Motor control is fundamental to the adaptive behaviour of natural and artificial systems, with one role being the production of active movement strategies to acquire and use key sensory information. A key neural component of motor systems are central pattern generators (CPGs) [1], for instance, those involved in the control of swimming movements of lamprey [2] or movement control in invertebrates [3]. CPGs have also been shown to be useful components for motor control in bio-inspired robots [4]. In insect brains, the Lateral Accessory Lobe is a key pre-motor area that has been shown to generate CPG like outputs in certain conditions. It is a conserved brain structure and is fundamental to a range of sensori-motor behaviours such as pheromone search in moths [5] and phonotaxis in crickets [6]. Computational models of the LAL have been developed to obtain a better understanding of how the LAL network can generate "flipflop" activity (Adden et al. (in prep.)) or how the LAL may contribute to pheromone plume tracking [7]. Here we develop a minimal spiking neural network model of the LAL, based on our previously developed general steering framework [8]. Our aim is to demonstrate that the model produces outputs that drive two distinct behavioural modes. Firstly, in the presence of sensory information it should output a steering signal that is proportional to that sensory information, so the location of a stimulus relative to the agent drives the steering. Secondly, in the absence of reliable sensory information, the network should produce a rhythmic output that can drive search patterns. We explore the adaptive properties of this network, by situating it in a simple Braitenberg-style animat (Fig. 1).

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Fig. 1. A: SNN architecture, CPG-neurons correspond to Type III neurons in the LAL, Output-neurons to Type I neurons. B: spatial familiarity function, left: one eye of the pair, right: cyclops, C: Agent configurations. Gray arrows depict direction of maximum familiarity. Left = BB, Middle = Cyclops, Right = BBCPG. D: CPG output as Spike Density Function (SDF), top: low input (resulting in large zig-zag movements), bottom: high input (resulting in small zig-zag movements). E: CPG output space showing how unilateral input results in unilateral output and bilateral input results in flip-flopping.

2 Methods

In a 2D-simulation, we implement a Braitenberg-Agent approaching a beacon. A Braitenberg-vehicle is a simplistic model agent using primitive sensors which directly control actuators, making it an ideal platform to model taxis behaviours. The agent has one of two sensor types: 1. Braitenberg version: two sensors covering 180° each with an overlap of 90° (therefore a total coverage of 270°) and 2. Cyclops version: one sensor covering 360°. The spatial transfer function imitates a typical Rotational Image Difference Function (RIDF). 100 % familiarity is sensed if the beacon is straight ahead of the agent, approaching 25% (this is the typical approximate minimum value for a 360° rotary IDF) when the target is behind the agent (Cyclops), or 0% when outside the visual range (Braitenberg). The spatial resolution is restricted to 1°. The agent is controlled by a spiking neural network (SNN) that is based on the LAL architecture as described in Steinbeck et al. 2020 [7]. The input neurons (leaky integrate & fire [LIF]) are driven by the sensor signal and excite the ipsilateral CPG- and output-neurons.

Author Proof



Fig. 2. A: one exemplary trial of Cyclops, top: familiarity, middle: Neuron spike density, bottom: heading and speed, B-D: paths and endpoints; B: Braitenberg, C: Cyclops, D: BBCPG, E: Endpoint distribution of left: BB, middle: Cyclops, right: BBCPG

The CPG neurons (adapting LIF) inhibit the contralateral CPG- and outputneurons. The output-neurons (LIF) excite the contralateral force neurons, which translate spikes into force (integration neurons, where activity represents acceleration). An imbalance of produced force leads to rotation. The SNN is tested in three versions: Braitenberg vehicle (BB), Cyclops and Braitenberg with CPG (BBCPG). The synaptic weights are the same for the same connections in all networks. The oscillation dynamics of the CPG are such that with low symmetric input the oscillation is slow and with strong symmetric input the oscillation is fast. Unilateral input results in no oscillation (Fig. 2).

3 Results

Each of 300 simulations was run for 3000 timesteps, and had a random initial starting position (15 units from the beacon) and heading. The trial was stopped if the agent reached the beacon. Each vehicle version was run 300 times. The BB vehicle converged towards the beacon if one sensor detected it at the beginning. If the beacon is in the agent's blind spot, it runs off into the approximate initial heading direction (which is due to spontaneous neuron activity). The distribution of endpoints is divided into two major clusters, one beyond the starting

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position, the other close to the beacon. The Cyclops converges towards the beacon in most trials, with only a low percentage running away. Due to the sinuous movements, a large area is covered. Almost all endpoints are located between the starting position and the beacon, therefore it is more successful than BB. The Braitenberg-CPG version converges towards the beacon in each trial. If it does not detect the beacon initially, the CPG driven small scale search steers the agent around (driven by Type III activity), until the stimulus becomes available and the proportional steering mode takes over (mediated by Type I neurons). The endpoints exhibit a smaller mean distance to the goal than in the other conditions.

4 Discussion

We have developed a spiking neural network model of an insect-inspired CPG which is used to underpin the steering behaviour of a Braitenberg-like vehicle. We show that a Braitenberg-only setup, or familiarity modulated CPG, have limited success navigating towards a beacon, while combining these approaches increases success. In future the system will be explored in terms of its biological plausibility to better understand the LAL network and it connection to other brain regions [10] and in more realistic scenarios we will investigate if this framework can improve navigation algorithms.

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Declaration

I, Fabian Steinbeck, hereby declare that this thesis has not been and will not be, submitted in whole or in part to another university for the award of any other degree.

Signature ____

Neuss, the 13.09.2022