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Corresponding Author: Florent Le Moël, Centre de recherches sur la cognition animale, Toulouse, FRANCE

Highlights

- The field of insect navigation is a good example of the implementation of Marr's three levels of explanation.
- It illustrates how important it is to consider an intermediary 'computational' level between neurons and behaviour.
- Ethological background and computational modelling both have been key to characterize this intermediary level.
- Recent descriptions of neural circuits can be well mapped to such identified computation level, rather than directly to behaviour.
- This led to multi-level understandings of complex insect navigational behaviours, of which we provide examples here.

Abstract

To understand the brain is to understand behaviour. However, understanding behaviour itself requires consideration of sensory information, body movements and the animal's ecology. Therefore, understanding the link between neurons and behaviour is a multi-level problem, which can be achieved when considering Marr's three levels of understanding: behaviour, computation, and neural implementation. Rather than establishing direct links between neurons and behaviour, the matter boils down to understanding two transitions: the link between neurons and brain computation on one hand, and the link between brain computations and behaviour on the other hand. The field of insect navigation illustrates well the power of such two-sided endeavour. We provide here examples revealing that each transition requires its own approach with its own intrinsic difficulties, and show how modelling can help us reach the desired multi-level understanding.

Keywords: insects, navigation, modelling, neuroethology

Introduction

Behaviour, like any natural phenomena, is entwined in the universe. To 'explain' behaviour, an arbitrary amount of levels (or scales) of explanation may be invoked, from the interactions between atoms to long-term influences of the surrounding ecosystems. The choice of levels of course depends on one's question. The typical neuroscience approach tries to establish direct causal links between the level of 'neurons' and the level of the 'individual's behaviour'. This endeavour can be quite

problematic, as understanding 'how brain produces behaviour' cannot be achieved by solely studying the neural circuitry [1], but requires first a good understanding of the animal's behaviour itself, which, most of the time, is lacking [2], [3]. In response to this problem, Marr has suggested that one should consider a third, intermediate, level between neurons and behaviour: the 'computational level [3], [4]. Considering three levels implies understanding two transitions: from neurons to computation, and from computation to behaviour.

Here, we show that the field of insect navigation, with its strong ethological background, has naturally implemented this three-level approach while seeking how brains relate to behaviour. Neural mappings in various insect species have been vital in developing recent computational models and behavioural data from other species have been vital in linking them to ecologically-relevant behaviour. This combination of approaches makes the field of insect navigation an interesting example case to help us identifying the possible difficulties and solutions towards a multi-level understanding from neurons to behaviour.

Three levels to bridge neurons and behaviour

The variety of approaches to insect navigation can be mapped to Marr's proposed three levels [4].

Level 3: Behaviour

The level 3 corresponds to the ecologically relevant behaviour itself. Thanks to its ethological background [5]–[7], the field of insect navigation is rich in such examples: the long-range migrating prowess of Monarch butterflies; the efficient visit of multiple flower patches by bumblebees; or the impressive homing abilities of desert ants after kilometre-long foraging bouts, are few examples. The key is here that the behaviour is observed in the field and interpreted in the light of the species natural tasks.

Level 2: Computation

The 'computation level' comprises the relationship between 'computational modules', which may (or may not) be mapped to brain areas. These functional modules interact together with the body and environment to extract information, to store it, and to produce motor outputs. The computation level can be used to explain behaviour, without the need to consider the neural implementation level. For instance, homing behaviour may result from a process of path integration (reviewed in [8]), which requires computational modules such as an internal compass, an odometer, and the integration of both into a homing vector to influence the animal's course. Often, if not always, interactions between computational modules, the body and the environment, show emergent properties: meaning that behaviour cannot be reduced to the understanding of a single module studied in isolation.

Level 1: Neurons

The neural implementation level refers to the actual connectivity at the scale of neurons or groups of neurons. The aim being to explain 'computational module' rather than behaviour. For instance, the insects' internal compass (i.e., a computational module) has been shown to emerge from a subset of neurons organised into what is called a ring attractor [9]. Here again, groups of neurons typically show emergent properties – which cannot be grasped when looking at single neurons only– that allow the above level ('computation') to emerge.

The need for models

Three levels imply two transitions (level 3 <-> level 2 <-> level 1), and understanding a transition requires a so-called 'model' [10]. A model, as we mean here, is not necessarily an algorithm run by a computer (computational model), it can simply use words. However, as we will see, computational models are key to explore the non-linear dynamics of brain-body-environment interactions. In any case, to provide a cross-level 'understanding', the model must establish and clearly state rules that explain how the desired proprieties at a given level emerge from the assumptions at the level below. We next provide examples of how models can help us understand both types of transitions.

Models from 'Behaviour' to 'Computation' (level 3 <-> level 2)

Understanding behaviour is far from trivial, as it is not merely a consequence of brain activity, but emerges from a complex system forming a closed loop involving dynamics between the animals' brain, body and environment, a phenomenon that is crucial yet often overlooked [11], [12]. These processes are hard to intuit because the interactions usually happen in parallel and are typically non-linear. In addition, each element of the system (i.e. the brain, body posture and perceived environment) is constantly changing, adding in complexity. Understanding behaviour also requires consideration of the individuals' Umwelts, that is, their personal experience through their specific sensory (e.g., polarised light sensing, panoramic vision or chemosensing) and motor (e.g., crawling, running or flying) systems, as well as the natural environment in which they have evolved [2], [7], [13].

The best way to understand how a behaviour is produced is therefore to start with a question stemming from the observation of the animal's behaviour in its natural environment. Once the ecological task of the animals defined, one can try to characterise what types of computations can explain such a behaviour, with an emphasis on its sensory-motor systems (its specific Umwelt). Such an approach has motivated more than 100 years of behavioural experimentation in insect navigation, literally decomposing the insects' impressive navigational feats into ever finer and more powerful mechanistic 'models'. Importantly, because of the endorsement of a naturalistic approach and the lack of neural data, the vast majority of these models was not neuroanatomically constrained. We believe this was a blessing rather than a problem because it led the field to focus on the level 3 <-> level 2 transition without being burdened by too many neural data. As we will see, the level 3 <-> level 2 transitions typically invoke explanations and rules that are entirely different from the ones at the levels below.

Various insect navigational behaviour have been investigated with such an approach: path integration [14], the use of learnt terrestrial cues [15], wind and olfaction [16], [17], obstacle avoidance [18], route optimisation [19], [20], sequence learning [21], [22] or navigation backwards [23], [24]. Below, we focus on behavioural models of route following and visual homing in ants and bees, because these illustrate well the importance of considering the 'brain-body-environment' dynamics at play.

Using views to navigate: modelling the brain-body-environment loop

Ants and bees are known to use learnt visual cues to follow routes and return to places of interest [25]–[27]. Seminal behavioural experiments demonstrated the use of egocentric views in bees and ants, and suggested models for how movement towards the goal could be achieved using egocentric visual memories [28], [29]. Later on, a key piece of information was brought by studying the natural environment through low-resolution panoramic pictures with the attempt to approximate the

insect's point of view (approaching its Umwelt): natural scenes, when compared as a whole through the insect eyes' low-resolution insect, provide remarkably robust directional information, which can be obtained by simply rotating on the spot [30]. Subsequent behavioural experiments quickly confirmed that ants just do so: they use panoramic visual cues [31]–[34], and display physical rotations -such as saccades and scanning- to recover directions [35]–[37]. Computational models implementing these ideas revealed that route following would spontaneously emerge in complex environments given remarkably simple guidance rules and little memory space [38]. But what about pinpointing the nest? Here again, a solution came from observations of the insect's body rather than the brain. Detailed studies of the choreographies displayed by ants, bees and wasps when leaving their nest –so called 'learning walks' or 'learning flights'– revealed that insects position their body in specific orientations relative to the nest for learning [39]–[44]. Adding these behavioural routines to the previously mentioned route-following models was enough for a pinpointed nest search to emerge. Additional motor routines, such as the continuous lateral oscillations observed in insects [35], [43], [45]–[47], or the fact that ants look regularly away from the nest [40] enabled further improvement of the navigational efficiency [48], [49]. The viability of these models was further strengthened by the fact that they equally captured a range of insect behavioural signatures, even though they were not designed to do so [47], [48], [50].

Taken together these various models led to an understanding of behaviour that arose from the study of the animals' movements and environment, rather than from looking at the brain. The simple rules identified lead to the emergence of impressive navigational feats only when embedded in an agent in closed loop with its environment and displaying the appropriate motor routines during learning (which is absolutely not trivial without computer simulations) [51]. Whether one could have reached such an understanding by focusing on the brain's circuitry –or by identifying direct causal links between brain activity and behaviour– is very unlikely, if not fundamentally impossible [1], [51]. In any case, we are now left with clear computational requirements for the brain. How can neurons achieve these requirements has not much to do with the above understanding, and requires an entirely different explanation at the level below.

Models from neurons to computational modules (level 2 <-> level 1)

An alternative – but complementary path to the one mentioned above can be followed, one that takes an opposite stance and is constrained by the lower levels: one may wonder how the identified 'computational modules' are implemented within the brain, being less concerned with behaviour. This is actually a quite different question from the daunting "How do neurons drive behaviour?". Understanding this transition, from neurons to computational modules, also requires models, especially when one considers the overwhelming amount of connectivity data available [box 1].

How to obtain the current view's familiarity?

Let us pursue with the example of route following and homing. One of the computational modules identified at the above level require to enable to memorise visual information from the scene experienced, as well as to output the familiarity of a current view. A solution at the neural level came from a model of the flies and honeybees' brain structure called Mushroom Bodies (MB). This model was originally designed to explain how neurons in this structure could support the learning and memories of odours [52], [53], but researchers in insect navigation realised that this neural model, provided with visual input, could equally explain the learning and memories of panoramic visual scenes, as well as how memorised and currently perceived scenes are compared to output a familiarity signal [54], [55]. In other words, the circuitry of the MB naturally achieves the desired

computational function identified by behavioural research on route following and homing. Establishing a direct link between MB and route following, without prior knowledge that such computational functions are sufficient for the navigational behaviour to emerge could have probably been achieved by direct neurobiological manipulation, however, in no case the knowledge of such a causal link would have brought understanding of the mechanism at play.

Together, this provides us with a truly multi-level understanding, from neurons to computation, and from computation to behaviour. Whether this understanding is correct regarding insects can be tested. Then comes the time for an experimental demonstration of a causal link from neurons to behavior (this being only achieved post-hoc and based on a prediction drawn from this understanding of the intermediary computational level, [box 3]). It turned out, while we wrote this review, two studies did indeed test and support these models' predictions by using pharmaceutical injections in ant's MB to demonstrate the expected roles of this brain area in ant visual navigation [56], [57].

How to build a good internal compass?

The behavioural approach has demonstrated that multiple behaviours such as path integration in ants and bees [14], [58] – or walking in a straight direction as observed when dung beetles try to run away with their ball of dung [59] – result from the integration of multiple directional cues, such as terrestrial, celestial, wind-based and self-motion cues, into a single but remarkably robust sense of direction [60]–[63]. Now that the need for such a computational feat has been behaviorally demonstrated, the question of how it can be implemented in an insect brain arises.

The insects Central Complex (CX), a central neuropil well conserved across arthropods species, had long been known for being implicated in navigation, but it is only recently that details on the compass implementation have been revealed [64]. Seelig and Jayaraman [65] showed with neuroimagery that a bump of neural activity shifting around a toroidal structure (the Ellipsoid Body of the CX) could encode and track the individual's current direction, not without recalling older theoretical models of 'ring-attractor' networks [66]–[69]. We now understand how a stable heading emerges in this brain structure from multi-modal neural signals [70, p. 201], [71]–[75].

Here again, this example shows how multi-level understanding arises from entirely different research approaches united by the identification of the intermediate computation module: how various natural behaviours emerge from an internal compass (in interaction with other computational modules) on one hand, and how such an internal compass representation emerges from a neural population on the other hand.

Closing the loop: Models from neurons to behaviour (level 3 <-> level 2 <-> level 1)

Considering nowadays' computing power, the idea of a fully functional simulation of a whole brain is considered as a next step for many [76]. However, we argue that this view is still far from realistic [box 3]. In many situations one should restrain a given model to the transition between two levels only. Indeed, adding levels complexifies the modelling effort, while not necessarily bringing additional insights, and may also result in a 'black box' effect [boxes 1, 2 and 3]. If not for additional insights, is it useful to design computational models from neurons to behaviour?

So long as one has acquired a multi-level understanding through models at both transitions 1 <-> 2 and 2 <-> 3, it can be useful to try and see if the neuron-to-behaviour model (1-2-3) works, as a proof

of concept. For instance, Stone et al. [77] successfully modelled path integration by embedding a biologically constrained neural model combining compass and distance information in a navigating agent. This proof of concept is important, as unexpected phenomena may emerge when complex neural dynamics are integrated to the complex brain-body-environment dynamics. Sometimes this is good news. In the case of this Path integration model, the authors were surprised to see that path integration worked irrespectively of the relation between the insect body orientation and direction of movement; a phenomenon that was actually reported in insects [78], [79].

Another advantage of such integrative models is that, if the model does work, it can then be used to make predictions about the neural activity in relation to specific behavioural situations [77], something which would be difficult to obtain without an integrative model. Similarly, it becomes possible to predict the emergence of specific behaviours given specific neural signatures. Both types of predictions can then be tested by respectively recording and stimulating neurons of navigating animals.

Multi-level models can also be of interest for predicting how differences in neural connectivity between species may explain respective behavioural optimisations to their ecological needs [55]. For example [80] show how slight differences in the Central Complex connectivity between locusts and fruit flies, and may gift the first with a compass more resilient to noise (i.e. suitable for long-distance migration) and the second with a compass that is faster in responding to changes in direction (i.e. allowing fast body saccades).

Finally, combination of behavioural, computational and neural models enables to understand how same brain structures can be implicated in drastically different navigational behaviours and as a corollary, how the stunning variety of behaviours observed across species can arise from very similar brains [9], [55], [81]. The fact that neural data from different insect species converges makes sense in this light: switching from one behaviour to another can be achieved by changing the body, the sensory system or how brain modules interact, and does not necessarily requires additional computational modules.

Conclusion

The current tools of neurobiology are undeniably useful, but their usefulness appears sublimed when exploited as a second step, after one has achieved a good understanding of how computational modules might interact to produce a given behaviour. We think that the study of navigation in insects still benefits from the advantage of its rich naturalistic background which pervades today's behavioural, computational and neuroscience research, and we hope that this ecological relevance will survive the modern upsurge of neurobiological data.

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[BOX 1: 'Why we cannot be purely bottom up']

One might expect to be able to extrapolate a fully functional model from full-brain connectomics only, 'ideally' by feeding all the lower level data to a computer, press 'play', and being able to observe the emerging behaviour. This kind of approach may appear as the perfectly objective, purely bottom-up model, but it turns out not to be that practical, and perhaps fundamentally impossible. First, we still lack key information about neurons (synapse gain, plasticity rules, etc.); and to model neurons perfectly accurately, we would need equally accurate models of the underlying molecular interactions, and so on, leading an impossible reduction. Second, for behaviours to emerge one would also need to model the body and the environment experienced, although this can be bypassed by embedding the model in a robot exposed to the real environment. But let us imagine our description of a given bee's body and brain circuits is exhaustive and perfectly accurate and our robotic technology advanced enough to make this approach possible. A robot-bee based on these data is constructed, the experimenter presses 'play' and it works, navigating and reacting just as well as a bee would… Now, question about the usefulness of such an approach arise: what understanding did we actually gain? Not much. We could then tweak the robot using diverse interventionist approaches in order to understand it better, but we would find ourselves basically right back where we were initially with the real bee. "The best material model for a cat is another, or preferably the same cat" [82] but then the model, because it does not bring any simplification of the object, brings no understanding. We thus need to concentrate our efforts towards achieving models that are simple enough to allow us to understand the rules at play. But if the model is a simplification, it should concern only a 'subset of the animal', a specific function, at a specific level of explanation. We therefore should always have an a-priori idea of the specific function we want to explain. In other words, a pinch of top-down thinking will always be necessary.

[BOX 2: 'What about Artificial Neural Networks?']

Models taking biological constraints at both the higher level and the lower level are best exemplified by ANNs: the goal function (the behaviour) is constrained at one end, the cells activity is constrained at the other, but the connectivity in between is not; these provide a sort of direct neuron-to-behaviour links (levels 1-3). The work is then to understand the type of computation (level 2) that might have emerged from various learning rules. Even though machine learning can be thought unsuited to study network structure of biological systems (only the cell-level response properties are similar to biology), such explorations have proven insightful. First, the emergence of computational modules can still bring insights on how the original complex behaviour may be decomposed into sub-components. Second, one can observe the emergence of elements otherwise observed in real biological systems such as ring-like organization and existence of shifter neurons for compass orientation [83], or neurons reminiscent of grid cells for navigation tasks [84].

Why does it work? Is it on the idea that both evolution and the ANNs should converge on the best connectivity? If that is so, one should keep in mind the constraints that are at play with evolution and not with ANN: the historical constraints. Evolution does not start from scratch, but modifies previously existing brains. Also, contrary to ANN, animals need to maintain a vast amount of functions simultaneously, and the resulting solution for the animal may well be different than the simple pooling of several functions optimised independently.

[BOX 3: 'About modelling multiple levels…']

If one should stick to model transitions between two levels only, should we ever model how full-fledged behaviours in the world emerge from neurons? Modelling through multiple levels at once can drastically increase the number of parameters. Such increased complexity, on top of exposing to a higher risk of biases and errors, bears one fundamental pitfall: it makes the modelling effort drift away from the possible insights it should bring. What good is a model that is as complex as the organism it is supposed to explain? [box 1]. To our opinion, modelling through multiple levels at once should be achieved only 'when needed'. For example, when modelling the transition from neurons to 'brain computation', lower levels such as ions movement that generate action potentials might preferably be abstracted if simpler 'spiking rates' values are good enough for the desired brain computation to emerge. However, there might be a 'need' to model single spikes if for instance, spike-timing dependant processes are key for the brain computation to emerge. This simplification step enables to identify the key elements for the desired process to emerge, that is, to understand well the transition. To sum up, if the lower level can be approximated by an existing assumption, this assumption should be preferred: the lower-level axioms of one field are the upper-level research goals of others.

[BOX 4: 'Integrating multiple cues']

Some models have focused on the integration of multiple cues or multiple navigation strategies such as path integration and learnt views into a single motor output. Behavioural experiments have shown that this integration is achieved continuously and optimally based on the relative certainty of the cues [85]–[90], and subsequent mathematical formalisation of the suggested computation have demonstrated that it could indeed fit the various observed data [91]–[94], as well as suggested how this type of computation could be implemented in the insect's brain [95]. Within Marr's 3 level framework, this endeavour stands clearly as an attempt to explain behaviour from the interaction between computational modules, that is, the transition between level 3 and 2. However, while other work aimed at identifying the computational modules underlying the emergence of a given navigational strategy (i.e., path integration *or* the use learnt view), here the computational modules are the navigational strategies per se (i.e., path integration *and* learn view). Therefore, the explanatory framework of this line of work can be viewed as standing one hierarchical level above. Even though biological relevance of the implementation (level 1 <-> level 2) is disregarded, these models, taken together, provide a good example of the complexity of the transition from computation to behaviour, and explain how behaviours can be decomposed into several levels of computations.

Bibliography

•• [1] E. Jonas and K. P. Kording, 'Could a Neuroscientist Understand a Microprocessor?', *PLoS Comput Biol*, vol. 13, no. 1, p. e1005268, Jan. 2017, doi: 10.1371/journal.pcbi.1005268. Authors apply several neuroscience techniques to a microprocessor controlling a program, as if it were a brain controlling behaviours, revealing that the reductionist approach is far from allowing one to understand behaviour.

•• [2] A. Gomez-Marin and A. A. Ghazanfar, 'The Life of Behavior', *Neuron*, vol. 104, no. 1, pp. 25–36, Oct. 2019, doi: 10.1016/j.neuron.2019.09.017. This paper advocates for the importance of the behavioural research in neuroscience, with a focus on the importance of the brain-body-environment closed-loop system.

•• [3] J. W. Krakauer, A. A. Ghazanfar, A. Gomez-Marin, M. A. MacIver, and D. Poeppel, 'Neuroscience Needs Behavior: Correcting a Reductionist Bias', *Neuron*, vol. 93, no. 3, pp. 480–490, Feb. 2017, doi: 10.1016/j.neuron.2016.12.041. This perspective paper highlights many important aspects of the neuroscience bias, the problems this creates, and pitfalls one should avoid in order to understand the brain.

[4] D. Marr, 'Vision: A computational investigation into the human representation and processing of visual information, henry holt and co', *Inc., New York, NY*, vol. 2, no. 4.2, 1982.

•• [5] R. Wehner, 'Early ant trajectories: spatial behaviour before behaviourism', *J Comp Physiol A*, vol. 202, no. 4, pp. 247–266, Apr. 2016, doi: 10.1007/s00359-015-1060-1.
Rüdiger Wehner retraces the historical background of ant navigation and highlights the solid grounds of behavioural research in the field.

[6] R. Menzel, 'A short history of studies on intelligence and brain in honeybees', *Apidologie*, Aug. 2020, doi: 10.1007/s13592-020-00794-x.

[7] A. Wystrach and P. Graham, 'What can we learn from studies of insect navigation?', *Animal Behaviour*, vol. 84, no. 1, pp. 13–20, Jul. 2012, doi: 10.1016/j.anbehav.2012.04.017.

• [8] S. Heinze, A. Narendra, and A. Cheung, 'Principles of Insect Path Integration', *Current Biology*, vol. 28, no. 17, pp. R1043–R1058, Sep. 2018, doi: 10.1016/j.cub.2018.04.058.
A recent, complete and detailed review on Path Integration in insects, from the behavioural significance to the neural correlates.

• [9] A. Honkanen, A. Adden, J. da Silva Freitas, and S. Heinze, 'The insect central complex and the neural basis of navigational strategies', *The Journal of Experimental Biology*, vol. 222, no. Suppl 1, p. jeb188854, Feb. 2019, doi: 10.1242/jeb.188854.
Recent and very complete review of the insect navigational behaviours that are based on path integration and compass representation.

[10] B. Webb, 'Can robots make good models of biological behaviour?', *Behav Brain Sci*, vol. 24, no. 6, pp. 1033–1050, Dec. 2001, doi: 10.1017/S0140525X01000127.

[11] R. D. Beer, '6 - The Dynamics of Brain–Body–Environment Systems: A Status Report', in *Handbook of Cognitive Science*, P. Calvo and A. Gomila, Eds. San Diego: Elsevier, 2008, pp. 99–120.

[12] A. Clark, *Being There: Putting Brain, Body, and World Together Again*. MIT Press, 1998.

[13] J. von Uexküll, *Umwelt und Innenwelt der Tiere*. Berlin, Heidelberg: Springer Berlin Heidelberg, 1921.

[14] T. S. Collett, 'Path integration: how details of the honeybee waggle dance and the foraging strategies of desert ants might help in understanding its mechanisms', *Journal of Experimental Biology*, vol. 222, no. 11, Jun. 2019, doi: 10.1242/jeb.205187.

[15] P. Graham and A. Philippides, 'Vision for navigation: What can we learn from ants?', *Arthropod Structure & Development*, vol. 46, no. 5, pp. 718–722, Sep. 2017, doi: 10.1016/j.asd.2017.07.001.

[16] C. Buehlmann, P. Graham, B. S. Hansson, and M. Knaden, 'Desert ants use olfactory scenes for navigation', *Animal Behaviour*, vol. 106, pp. 99–105, Aug. 2015, doi: 10.1016/j.anbehav.2015.04.029.
[17] H. Wolf and R. Wehner, 'Pinpointing food sources: Olfactory and anemotactic orientation in desert ants, Cataglyphis fortis', *Journal of Experimental Biology*, vol. 203, no. 5, pp. 857–868, 2000, doi: 10.5167/uzh-636.
[18] Y. Baba, A. Tsukada, and C. M. Comer, 'Collision avoidance by running insects: antennal guidance in cockroaches', *J. Exp. Biol.*, vol. 213, no. Pt 13, pp. 2294–2302, Jul. 2010, doi: 10.1242/jeb.036996.
[19] A. Buatois and M. Lihoreau, 'Evidence of trapline foraging in honeybees', *The Journal of Experimental Biology*, vol. 219, no. 16, pp. 2426–2429, Aug. 2016, doi: 10.1242/jeb.143214.
[20] A. Wystrach, C. Buehlmann, S. Schwarz, K. Cheng, and P. Graham, 'Rapid Aversive and Memory Trace Learning during Route Navigation in Desert Ants', *Current Biology*, p. S096098222030289X, Apr. 2020, doi: 10.1016/j.cub.2020.02.082.
[21] T. S. Collett, S. N. Fry, and R. Wehner, 'Sequence learning by honeybees', *J Comp Physiol A*, vol. 172, no. 6, Jun. 1993, doi: 10.1007/BF00195395.
[22] D. Macquart, G. Latil, and G. Beugnon, 'Sensorimotor sequence learning in the ant Gigantiops destructor', *Animal Behaviour*, vol. 75, no. 5, pp. 1693–1701, May 2008, doi: 10.1016/j.anbehav.2007.10.023.
[23] M. Collett, P. Graham, and T. S. Collett, 'Insect Navigation: What Backward Walking Reveals about the Control of Movement', *Current Biology*, vol. 27, no. 4, pp. R141–R144, Feb. 2017, doi: 10.1016/j.cub.2016.12.037.
[24] S. Schwarz, L. Clement, E. Gkanias, and A. Wystrach, 'How do backward walking ants (*Cataglyphis velox*) cope with navigational uncertainty?', Animal Behavior and Cognition, preprint, Dec. 2019. doi: 10.1101/2019.12.16.877704.
[25] M. Kohler and R. Wehner, 'Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors?', *Neurobiology of Learning and Memory*, vol. 83, no. 1, pp. 1–12, Jan. 2005, doi: 10.1016/j.nlm.2004.05.011.
[26] M. Mangan and B. Webb, 'Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*)', *Behavioral Ecology*, vol. 23, no. 5, pp. 944–954, 2012, doi: 10.1093/beheco/ars051.
[27] M. Collett, L. Chittka, and T. S. Collett, 'Spatial memory in insect navigation', *Curr. Biol.*, vol. 23, no. 17, pp. R789-800, Sep. 2013, doi: 10.1016/j.cub.2013.07.020.
[28] B. A. Cartwright and T. S. Collett, 'Landmark learning in bees: Experiments and models', *J. Comp. Physiol.*, vol. 151, no. 4, pp. 521–543, 1983, doi: 10.1007/BF00605469.
[29] R. Wehner and F. Räber, 'Visual spatial memory in desert ants, *Cataglyphis bicoior* (Hymenoptera: Formicidae)', *Experientia*, vol. 35, no. 12, pp. 1569–1571, Dec. 1979, doi: 10.1007/BF01953197.
[30] J. Zeil, M. I. Hofmann, and J. S. Chahl, 'Catchment areas of panoramic snapshots in outdoor scenes', *J. Opt. Soc. Am. A*, vol. 20, no. 3, p. 450, Mar. 2003, doi: 10.1364/JOSAA.20.000450.
[31] P. Graham and K. Cheng, 'Ants use the panoramic skyline as a visual cue during navigation', *Current Biology*, vol. 19, no. 20, pp. R935–R937, Nov. 2009, doi: 10.1016/j.cub.2009.08.015.
[32] R. Wehner and M. Müller, 'Piloting in desert ants: pinpointing the goal by discrete landmarks', *Journal of Experimental Biology*, vol. 213, no. 24, pp. 4174–4179, Dec. 2010, doi: 10.1242/jeb.050674.
[33] A. Wystrach, K. Cheng, S. Sosa, and G. Beugnon, 'Geometry, features, and panoramic views: Ants in rectangular arenas.', *Journal of Experimental Psychology: Animal Behavior Processes*, vol. 37, no. 4, pp. 420–435, Oct. 2011, doi: 10.1037/a0023886.
[34] A. Wystrach, G. Beugnon, and K. Cheng, 'Landmarks or panoramas: what do navigating ants attend to for guidance?', *Frontiers in Zoology*, vol. 8, no. 1, p. 21, 2011, doi: 10.1186/1742-9994-8-21.

[35] T. S. Collett, D. D. Lent, and P. Graham, 'Scene perception and the visual control of travel direction in navigating wood ants', *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 369, no. 1636, p. 20130035, Feb. 2014, doi: 10.1098/rstb.2013.0035.

[36] D. D. Lent, P. Graham, and T. S. Collett, 'Phase-Dependent Visual Control of the Zigzag Paths of Navigating Wood Ants', *Current Biology*, vol. 23, no. 23, pp. 2393–2399, Dec. 2013, doi: 10.1016/j.cub.2013.10.014.

[37] A. Wystrach, A. Philippides, A. Aurejac, K. Cheng, and P. Graham, 'Visual scanning behaviours and their role in the navigation of the Australian desert ant *Melophorus bagoti*', *Journal of Comparative Physiology A*, vol. 200, no. 7, pp. 615–626, Jul. 2014, doi: 10.1007/s00359-014-0900-8.

[38] B. Baddeley, P. Graham, P. Husbands, and A. Philippides, 'A Model of Ant Route Navigation Driven by Scene Familiarity', *PLoS Computational Biology*, vol. 8, no. 1, p. e1002336, Jan. 2012, doi: 10.1371/JOURNAL.PCBI.1002336.

[39] P. N. Fleischmann, R. Grob, R. Wehner, and W. Rössler, 'Species-specific differences in the fine structure of learning walk elements in Cataglyphis ants', *Journal of Experimental Biology*, vol. 220, no. 13, pp. 2426–2435, Jul. 2017, doi: 10.1242/jeb.158147.

[40] P. Jayatilaka, T. Murray, A. Narendra, and J. Zeil, 'The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*', *The Journal of Experimental Biology*, vol. 221, no. 20, p. jeb185306, Oct. 2018, doi: 10.1242/JEB.185306.

[41] M. Müller and R. Wehner, 'Path Integration Provides a Scaffold for Landmark Learning in Desert Ants', *Current Biology*, vol. 20, no. 15, pp. 1368–1371, Aug. 2010, doi: 10.1016/j.cub.2010.06.035.

[42] A. Philippides, N. H. de Ibarra, O. Riabinina, and T. S. Collett, 'Bumblebee calligraphy: the design and control of flight motifs in the learning and return flights of *Bombus terrestris*', *Journal of Experimental Biology*, vol. 216, no. 6, pp. 1093–1104, Mar. 2013, doi: 10.1242/jeb.081455.

[43] W. Stürzl, J. Zeil, N. Boeddeker, and J. M. Hemmi, 'How Wasps Acquire and Use Views for Homing', *Current Biology*, vol. 26, no. 4, pp. 470–482, Feb. 2016, doi: 10.1016/j.cub.2015.12.052.

[44] J. Zeil, A. Kelber, and R. Voss, 'Structure and function of learning flights in ground-nesting bees and wasps', *Journal of Experimental Biology*, vol. 199, no. 1, pp. 245–252, Jan. 1996.

[45] L. P. S. Kuenen and T. C. Baker, 'A non-anemotactic mechanism used in pheromone source location by flying moths', *Physiological Entomology*, vol. 8, no. 3, pp. 277–289, 1983, doi: 10.1111/j.1365-3032.1983.tb00360.x.

[46] S. Namiki and R. Kanzaki, 'The neurobiological basis of orientation in insects: insights from the silkmoth mating dance', *Current Opinion in Insect Science*, vol. 15, pp. 16–26, Jun. 2016, doi: 10.1016/j.cois.2016.02.009.

[47] A. Wystrach, K. Lagogiannis, and B. Webb, 'Continuous lateral oscillations as a core mechanism for taxis in *Drosophila* larvae', *eLife*, vol. 5, p. e15504, Oct. 2016, doi: 10.7554/eLife.15504.

[48] A. Kodzhabashev and M. Mangan, 'Route Following Without Scanning', in *Biomimetic and Biohybrid Systems*, vol. 9222, S. P. Wilson, P. F. M. J. Verschure, A. Mura, and T. J. Prescott, Eds. Cham: Springer International Publishing, 2015, pp. 199–210.

[49] F. Le Möel and A. Wystrach, 'Opponent processes in visual memories: A model of attraction and repulsion in navigating insects' mushroom bodies', *PLOS Computational Biology*, vol. 16, no. 2, p. e1007631, Feb. 2020, doi: 10.1371/journal.pcbi.1007631.

• [50] T. Murray *et al.*, 'The role of attractive and repellent scene memories in ant homing (Myrmecia croslandi)', *Journal of Experimental Biology*, vol. 223, no. 3, Feb. 2020, doi: 10.1242/jeb.210021.
Using an air-cushioned treadmill, authors record the oscillations expressed by ants in several locations (familiar and unfamiliar). A complementary modelling approach is described, which explains the a-priori counter-intuitive results of the behavioural data.

• [51] B. Webb, 'The internal maps of insects', *J. Exp. Biol.*, vol. 222, no. Pt Suppl 1, 06 2019, doi: 10.1242/jeb.188094.

A review of insect navigational strategies that revolves around the 'computation' level, with good insights about the place of modelling.

[52] M. Heisenberg, 'Mushroom body memoir: from maps to models', *Nat Rev Neurosci*, vol. 4, no. 4, pp. 266–275, 2003, doi: 10.1038/nrn1074.

[53] D. Smith, J. Wessnitzer, and B. Webb, 'A model of associative learning in the mushroom body', *Biol Cybern*, vol. 99, no. 2, pp. 89–103, Aug. 2008, doi: 10.1007/s00422-008-0241-1.

• [54] P. Ardin, F. Peng, M. Mangan, K. Lagogiannis, and B. Webb, 'Using an Insect Mushroom Body Circuit to Encode Route Memory in Complex Natural Environments', *PLoS Comput Biol*, vol. 12, no. 2, Feb. 2016, doi: 10.1371/journal.pcbi.1004683.
Authors demonstrate that a model entirely inspired by biological connectivity -while keeping the lower layers of implementation totally abstracted- can allow for the computation needed for visual route following.

•• [55] B. Webb and A. Wystrach, 'Neural mechanisms of insect navigation', *Current Opinion in Insect Science*, vol. 15, pp. 27–39, Jun. 2016, doi: 10.1016/j.cois.2016.02.011.
In this relatively recent review, authors describe the state of the insect navigation research, how it principally comes from ethological studies and less from neural data, and argue that modelling may serve as a great tool to push the field forward.

[56] J. F. Kamhi, A. B. Barron, and A. Narendra, 'Vertical Lobes of the Mushroom Bodies Are Essential for View-Based Navigation in Australian Myrmecia Ants', *Current Biology*, vol. 30, no. 17, pp. 3432-3437.e3, Sep. 2020, doi: 10.1016/j.cub.2020.06.030.

[57] C. Buehlmann, B. Wozniak, R. Goulard, B. Webb, P. Graham, and J. E. Niven, 'Mushroom Bodies Are Required for Learned Visual Navigation, but Not for Innate Visual Behavior, in Ants', *Current Biology*, vol. 30, no. 17, pp. 3438-3443.e2, Sep. 2020, doi: 10.1016/j.cub.2020.07.013.

[58] A. Cheung, 'Animal path integration: A model of positional uncertainty along tortuous paths', *Journal of Theoretical Biology*, vol. 341, pp. 17–33, Jan. 2014, doi: 10.1016/j.jtbi.2013.09.031.

[59] M. Dacke and B. el Jundi, 'The Dung Beetle Compass', *Current Biology*, vol. 28, no. 17, pp. R993–R997, Sep. 2018, doi: 10.1016/j.cub.2018.04.052.

[60] M. Dacke *et al.*, 'Multimodal cue integration in the dung beetle compass', *Proc. Natl. Acad. Sci. U.S.A.*, vol. 116, no. 28, pp. 14248–14253, 09 2019, doi: 10.1073/pnas.1904308116.

[61] M. Müller and R. Wehner, 'Wind and sky as compass cues in desert ant navigation', *Naturwissenschaften*, vol. 94, no. 7, pp. 589–594, Jul. 2007, doi: 10.1007/s00114-007-0232-4.

[62] A. Wystrach, S. Schwarz, P. Schultheiss, A. Baniel, and K. Cheng, 'Multiple sources of celestial compass information in the Central Australian desert ant Melophorus bagoti', *J Comp Physiol A*, vol. 200, no. 6, pp. 591–601, Jun. 2014, doi: 10.1007/s00359-014-0899-x.

[63] A. Wystrach and S. Schwarz, 'Ants use a predictive mechanism to compensate for passive displacements by wind', *Current Biology*, vol. 23, no. 24, pp. R1083–R1085, Dec. 2013, doi: 10.1016/j.cub.2013.10.072.

[64] K. Pfeiffer and U. Homberg, 'Organization and Functional Roles of the Central Complex in the Insect Brain', *Annu. Rev. Entomol.*, vol. 59, no. 1, pp. 165–184, Jan. 2014, doi: 10.1146/annurev-ento-011613-162031.

[65] J. D. Seelig and V. Jayaraman, 'Neural dynamics for landmark orientation and angular path integration', *Nature*, vol. 521, no. 7551, pp. 186–191, May 2015, doi: 10.1038/nature14446.

[66] X. Sun, M. Mangan, and S. Yue, 'An Analysis of a Ring Attractor Model for Cue Integration', in *Biomimetic and Biohybrid Systems*, vol. 10928, V. Vouloutsi, J. Halloy, A. Mura, M. Mangan, N. Lepora, T. J. Prescott, and P. F. M. J. Verschure, Eds. Cham: Springer International Publishing, 2018, pp. 459–470.

[67] D. S. Touretzky, 'Attractor network models of head direction cells', *Head direction cells and the neural mechanisms of spatial orientation*, pp. 411–432, 2005.

[68] W. E. Skaggs, J. J. Knierim, H. S. Kudrimoti, and B. L. McNaughton, 'A Model of the Neural Basis of the Rat's Sense of Direction', p. 10.

[69] P. Song and X.-J. Wang, 'Angular Path Integration by Moving "Hill of Activity": A Spiking Neuron Model without Recurrent Excitation of the Head-Direction System', *J. Neurosci.*, vol. 25, no. 4, pp. 1002–1014, Jan. 2005, doi: 10.1523/JNEUROSCI.4172-04.2005.
[70] V. G. Fiore, B. Kottler, X. Gu, and F. Hirth, 'In silico Interrogation of Insect Central Complex Suggests Computational Roles for the Ellipsoid Body in Spatial Navigation', *Front. Behav. Neurosci.*, vol. 11, 2017, doi: 10.3389/fnbeh.2017.00142.
[71] J. Green, A. Adachi, K. K. Shah, J. D. Hirokawa, P. S. Magani, and G. Maimon, 'A neural circuit architecture for angular integration in *Drosophila*', *Nature*, vol. 546, no. 7656, pp. 101–106, May 2017, doi: 10.1038/NATURE22343.
[72] K. S. Kakaria and B. L. de Bivort, 'Ring Attractor Dynamics Emerge from a Spiking Model of the Entire Protocerebral Bridge', *Front. Behav. Neurosci.*, vol. 11, Feb. 2017, doi: 10.3389/fnbeh.2017.00008.
[73] S. S. Kim, H. Rouault, S. Druckmann, and V. Jayaraman, 'Ring attractor dynamics in the *Drosophila* central brain', *Science*, vol. 356, no. 6340, pp. 849–853, May 2017, doi: 10.1126/science.aal4835.
[74] T.-S. Su, W.-J. Lee, Y.-C. Huang, C.-T. Wang, and C.-C. Lo, 'Coupled symmetric and asymmetric circuits underlying spatial orientation in fruit flies', *Nat Commun*, vol. 8, no. 1, p. 139, Dec. 2017, doi: 10.1038/s41467-017-00191-6.
[75] D. Turner-Evans *et al.*, 'Angular velocity integration in a fly heading circuit', *eLife*, vol. 6, p. e23496, May 2017, doi: 10.7554/eLife.23496.
[76] L. T. Collins, 'The case for emulating insect brains using anatomical "wiring diagrams" equipped with biophysical models of neuronal activity', *Biol Cybern*, vol. 113, no. 5, pp. 465–474, Dec. 2019, doi: 10.1007/s00422-019-00810-z.
•• [77] T. Stone *et al.*, 'An Anatomically Constrained Model for Path Integration in the Bee Brain', *Current Biology*, vol. 27, no. 20, pp. 3069-3085.e11, Oct. 2017, doi: 10.1016/J.CUB.2017.08.052. A fully bio-inspired model of the brain computations that are necessary to perform Path Integration is described. It allows for accurate reproduction of path integration in simulations, as well as other more specific behaviours such as holonomic movement and localised search patterns.
[78] S. E. Pfeffer and M. Wittlinger, 'How to find home backwards? Navigation during rearward homing of *Cataglyphis fortis* desert ants', *The Journal of Experimental Biology*, vol. 219, no. 14, pp. 2119–2126, Jul. 2016, doi: 10.1242/jeb.137786.
[79] J. Riley *et al.*, 'Compensation for wind drift by bumble-bees', *Nature*, vol. 400, no. 6740, p. 126, 1999, doi: 10.1038/22029.
[80] I. Pisokas, S. Heinze, and B. Webb, 'The head direction circuit of two insect species', Neuroscience, preprint, Nov. 2019. Accessed: Dec. 10, 2019. [Online]. Available: http://biorxiv.org/lookup/doi/10.1101/854521.
[81] A. Wystrach, 'Insect spatial learning, a stroll through Tinbergen's four questions.', in *Encyclopedia of animal behavior, 2019*, 2019.
[82] A. Rosenblueth and N. Wiener, 'The Role of Models in Science', *Philosophy of Science*, vol. 12, no. 4, pp. 316–321, Oct. 1945, doi: 10.1086/286874.
[83] C. J. Cueva, P. Y. Wang, M. Chin, and X.-X. Wei, 'Emergence of functional and structural properties of the head direction system by optimization of recurrent neural networks', *arXiv:1912.10189 [cs, q-bio, stat]*, Dec. 2019, Accessed: Jan. 03, 2020. [Online]. Available: http://arxiv.org/abs/1912.10189.
[84] A. Banino *et al.*, 'Vector-based navigation using grid-like representations in artificial agents', *Nature*, vol. 557, no. 7705, Art. no. 7705, May 2018, doi: 10.1038/s41586-018-0102-6.
[85] M. Collett, 'How Navigational Guidance Systems Are Combined in a Desert Ant', *Current Biology*, vol. 22, no. 10, pp. 927–932, May 2012, doi: 10.1016/j.cub.2012.03.049.
[86] E. L. Legge, A. Wystrach, M. L. Spetch, and K. Cheng, 'Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues', *Journal of Experimental Biology*, vol. 217, no. 23, pp. 4159–4166, 2014, doi: 10.1242/jeb.107862.

[87] P. Bregy, S. Sommer, and R. Wehner, 'Nest-mark orientation versus vector navigation in desert ants', *J. Exp. Biol.*, vol. 211, no. Pt 12, pp. 1868–1873, Jun. 2008, doi: 10.1242/jeb.018036.
[88] A. Wystrach, M. Mangan, and B. Webb, 'Optimal cue integration in ants', *Proceedings of the Royal Society B: Biological Sciences*, vol. 282, no. 1816, p. 20151484, Oct. 2015, doi: 10.1098/rspb.2015.1484.
[89] R. Wehner, 'The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae)', p. 12, 2009.
[90] C. Buehlmann, M. Mangan, and P. Graham, 'Multimodal interactions in insect navigation', *Anim Cogn*, Apr. 2020, doi: 10.1007/s10071-020-01383-2.
[91] H. Cruse and R. Wehner, 'No Need for a Cognitive Map: Decentralized Memory for Insect Navigation', *PLOS Computational Biology*, vol. 7, no. 3, p. e1002009, Mar. 2011, doi: 10.1371/journal.pcbi.1002009.
[92] T. Hoinville, R. Wehner, and H. Cruse, 'Learning and Retrieval of Memory Elements in a Navigation Task', in *Biomimetic and Biohybrid Systems*, Berlin, Heidelberg, 2012, pp. 120–131, doi: 10.1007/978-3-642-31525-1_11.
[93] R. Wehner, T. Hoinville, H. Cruse, and K. Cheng, 'Steering intermediate courses: desert ants combine information from various navigational routines', *J Comp Physiol A*, vol. 202, no. 7, pp. 459–472, Jul. 2016, doi: 10.1007/s00359-016-1094-z.
[94] T. Hoinville and R. Wehner, 'Optimal multiguidance integration in insect navigation', *PNAS*, vol. 115, no. 11, pp. 2824–2829, Mar. 2018, doi: 10.1073/pnas.1721668115.
[95] X. Sun, S. Yue, and M. Mangan, 'A Decentralised Neural Model Explaining Optimal Integration Of Navigational Strategies in Insects', *bioRxiv*, p. 856153, Mar. 2020, doi: 10.1101/856153.