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Florent Le Moël

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THÈSE

En vue de l'obtention du
DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE
Délivré par l'Université Toulouse 3 - Paul Sabatier

Présentée et soutenue par
Florent LE MOËL

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Thèse dirigée par

Antoine WYSTRACH

Jury

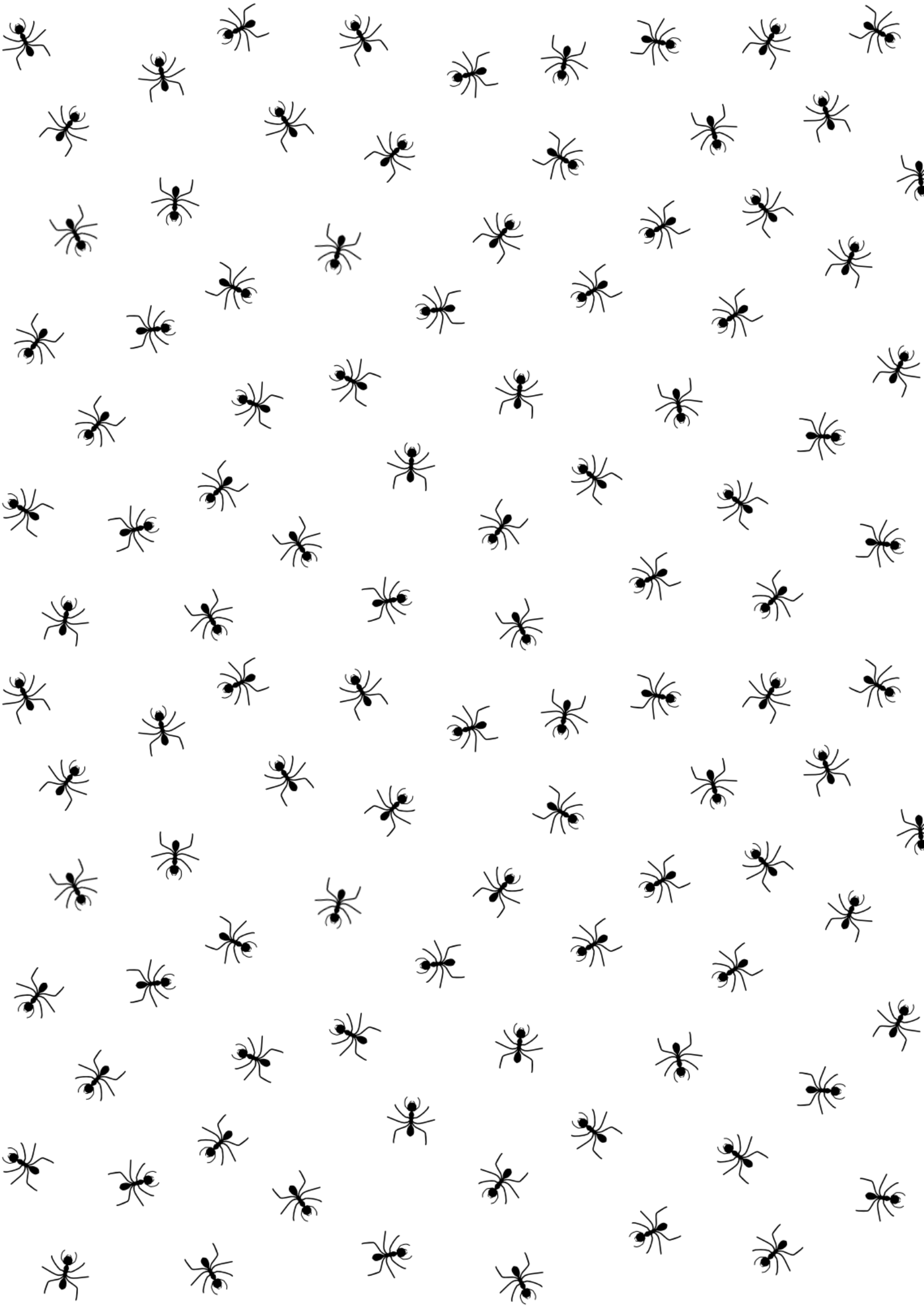
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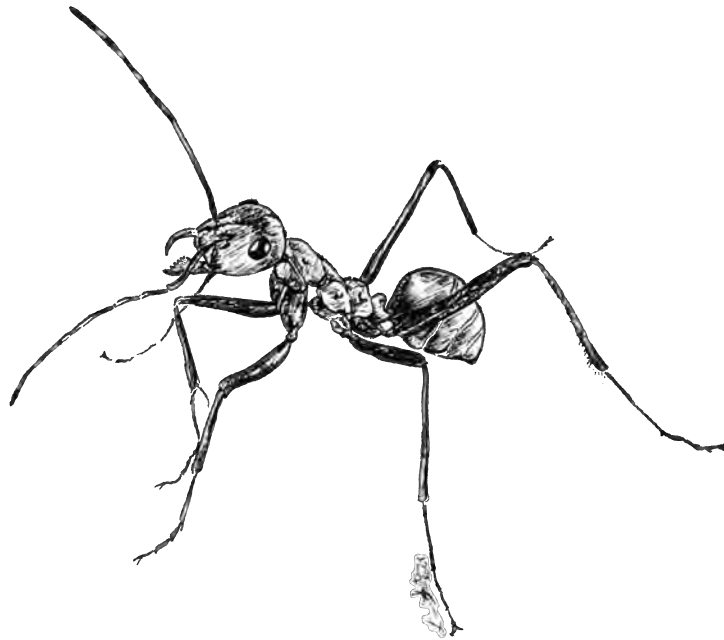
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Visual navigation in ants: a modelling approach

Paul Sabatier University - Toulouse III



Florent Le Moël

2021

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Abstract

Being able to navigate efficiently is crucial to the survival of many animals, including insects. Eusocial Hymenoptera are perfect models to study spatial cognition, because their ecological requirements (central-place foraging) precisely call for elaborate navigational skills. Among these studied Hymenoptera, desert ants occupy a place of choice owing to several advantages linked to the scale of their displacements and relatively short life cycles. The field of insect navigation, with its strong ethological and sensory physiology background, has generated a vast number of studies characterizing and describing various navigational strategies, with as general consensus that seemingly complex behaviours can actually often be explained by the interactions of much simpler strategies. Insect navigation has thus been benefitting from this wealth of behavioural data for a long time, but the recent advances in neurobiology allowing scientists to trace, record, and manipulate neurons at an increasingly large scale and precision, provided invaluable insights about the circuits underpinning complex behaviour. However, drawing direct links between the neural hardware and the behaviour is often not sufficient to reach a real understanding of the intricate dynamics involved. For this, formulating hypotheses in a theoretical framework is needed, and this can be done via a modelling approach.

This thesis thus presents such a computational approach, which aims to help unravel the links between brain and behaviour, and hopefully consolidating our general understanding of the mechanisms underlying insect navigation. It also presents computational and methodological tools to help other, future modelling efforts. All the computational models presented herein are constrained by biological truths on two levels: known neural circuitry on one hand and described behavioural signatures on the other hand. This allows the models to formulate tangible mechanistical understandings of how behaviour can emerge from the brain in closed loop with the environment. It also allows the models to generate predictions that can be verifiable experimentally, for both the neuroanatomical and behavioural levels.

We first investigate several vector-based navigational strategies displayed by insects, with a focus on a brain area called the Central Complex. The model suggests a plausible

mechanism for vector memory addition and subtraction and shows that vector manipulation is a highly parsimonious explanation to many navigational behaviours usually considered as requiring complex map-like representations, and that the known architecture of the insect Central Complex is equipped to perform such encoding and operations. Then we tackle view-based navigational strategies with a focus on the Mushroom Bodies, a brain area implicated in associative learning of various sensory modalities. A first model demonstrates that encoding a large number of complex views is possible in the Mushroom Bodies. It suggests how several visual processing steps, as well as several parameters in the Mushroom Bodies themselves, may play an important role in the way views are encoded. This encoding allows learning of long routes in complex environments. A second model of the Mushroom Bodies investigates how this specific encoding of the views, when generated with help of a well characterized active sensing routine, can yield a combined guidance from attractive and aversive memory pathways. This combined guidance information can be used directly to produce robust navigation without the need to sample multiple directions.

Finally, an overview of the importance of modelling in neuroethology is exposed, arguing that insect navigation is a very good example of such multidisciplinary approach. Hopefully, the work presented in this thesis will help contribute to our global understanding of the multi-level problematic that is how brain produces behaviour.

Résumé

Être capable de naviguer efficacement est essentiel à la survie de nombreux animaux, y compris pour les insectes. Les hyménoptères eusociaux sont des modèles parfaits pour étudier la cognition spatiale, car leurs exigences écologiques (fourragement avec point central / nid fixe) requièrent précisément des capacités élaborées en navigation. Parmi ces hyménoptères étudiés, les fourmis du désert occupent une place de choix en raison de plusieurs avantages liés à l'échelle de leurs déplacements et à des cycles de vie relativement courts. L'étude de la navigation des insectes, domaine avec un solide historique en éthologie et physiologie sensorielle, a produit un grand nombre d'études caractérisant et décrivant des stratégies de navigation variées. Ces études ont comme consensus général que des comportements apparemment complexes peuvent en fait souvent être expliqués par les interactions entre des stratégies beaucoup plus simples. L'étude de la navigation des insectes profite ainsi de cette richesse de données comportementales depuis longtemps, mais les progrès récents en neurobiologie permettant aux scientifiques de tracer, enregistrer et manipuler les neurones à une échelle et une précision de plus en plus fines, ont apporté d'incalculables perspectives sur les circuits sous-tendant ces comportements complexes. Cependant, établir des liens directs entre les circuits neuronaux et le comportement ne suffit souvent pas pour parvenir à une véritable compréhension des dynamiques complexes qui sont impliquées. Pour cela, il est nécessaire de formuler des hypothèses dans un cadre théorique, et cela peut se faire via une approche de modélisation.

Cette thèse présente une telle approche en modélisation informatique ayant pour but de contribuer à éclaircir les liens entre cerveau et comportement et, espérons-le, à consolider notre compréhension générale des mécanismes sous-jacents à la navigation des insectes. Elle présente également des outils informatiques et méthodologiques pour aider d'autres efforts de modélisation futurs. Tous les modèles présentés ici sont contraints par des vérités biologiques à deux niveaux : d'une part, par les circuits neuronaux connus, et d'autre part par les signatures comportementales décrites. Cela permet aux modèles de formuler des compréhensions mécanistiques tangibles sur la façon dont le comportement émerge du cerveau via les interactions avec l'environnement. Cela permet également aux modèles de générer des prédictions vérifiables expérimentalement, tant au niveau

neuroanatomique que comportemental.

Nous étudions d'abord plusieurs stratégies de navigation vectorielles manifestées par les insectes, en mettant l'accent sur une zone du cerveau appelée le Complexe Central. Le modèle suggère un mécanisme plausible pour l'addition et la soustraction de vecteurs, et montre que la manipulation vectorielle est une explication très parcimonieuse pour de nombreux comportements de navigation généralement considérés comme nécessitant des représentations complexes (de type 'carte mentale'), et que l'architecture connue du Complexe Central est adaptée pour effectuer cet encodage et ces opérations. Ensuite, nous abordons des stratégies de navigation basées sur la vue, en mettant l'accent sur les Corps Pédonculés, une zone du cerveau impliquée dans l'apprentissage associatif pour diverses modalités sensorielles. Un premier modèle démontre que l'encodage d'un grand nombre de vues complexes est possible dans les Corps Pédonculés. Il suggère comment plusieurs étapes de traitement visuel, ainsi que plusieurs paramètres dans les Corps Pédonculés eux-mêmes peuvent jouer un rôle important dans la façon dont les vues sont encodées. Cet encodage permet l'apprentissage de longues routes dans des environnements complexes. Un deuxième modèle des Corps Pédonculés étudie comment cet encodage spécifique des vues, lorsqu'il est réalisé à l'aide d'une routine d'échantillonnage actif bien caractérisée, peut produire une information de guidage combinée à partir de voies de mémoire attractives et aversives. Cette information de guidage combinée peut être utilisée directement pour produire une navigation robuste sans avoir besoin d'échantillonner toutes les directions.

Enfin, un aperçu de l'importance de la modélisation en neuroéthologie est exposé, soulignant que le domaine de l'étude de la navigation des insectes est un très bon exemple d'une telle approche multidisciplinaire. Espérons que le travail présenté dans cette thèse contribuera à notre compréhension globale de cette problématique à plusieurs niveaux qui est 'Comment le cerveau produit-il le comportement ?'.

Introduction

As a starting point, I would like to address the question that I hear most often from friends and family, which is: *“Why do you study insect navigation?”*

In terms of number of species, insects are the largest and most diverse group of all metazoans on Earth: more than 1 million species described and with a total number estimated between 5 and 10 million [209]: this represents more than all known vertebrates and plants species combined [241]. Correspondingly, they fulfil important ecological functions in most environments, as they inhabit almost any possible land and freshwater ecosystem found on the planet [322]. Without insects, human life would probably not be possible as ecosystems would potentially collapse [323]. Also, in terms of biomass, insects exceed vertebrates in most environments. That is especially true for ants, which can account for up to 25% of all animal biomass in terrestrial environments [247]. They are ubiquitous and they have been so for a long time: their estimated evolutionary age varies between 115 and 168 million years [181, 18], a testimony of their evolutionary success. This already sparks a great interest in any biologist’s mind but what makes insects especially fascinating to me is their brain. This tiny (typically less than 0.1 mm^3) piece of neural hardware is to me, even more beautiful than the brains of vertebrates, because of its incredible optimization: despite such limited brain matter (1 million times less neurons than us), insects achieve sophisticated behaviours and solve learning paradigms astonishingly well, even when compared to much larger-brained animals. In other words, the relatively small size of an insect brain does not limit the complexity of the tasks they can achieve [35], but is instead a prime example of optimisation and refinement through natural selection.

“There may be extraordinary mental activity with an extremely small absolute mass of nervous matter: thus the wonderfully diversified instincts, mental powers, and affections of ants are notorious, yet their cerebral ganglia are not so large as the quarter of a small pin’s head. Under this point of view, the brain of an ant is one of the most marvellous atoms of matter in the world, perhaps more so than the brain of a man.”

—Charles Darwin (1871) [51]

Desert ants such as *Cataglyphis*, *Ocymyrmex* or *Melophorus* are strict thermophilic diurnal scavengers [313, 305, 317, 36, 192]. Their physiological (e.g., heat shock proteins [78, 32]), morphological (e.g., long legs, slender bodies [311, 310, 259]) and behavioural (e.g., walking speed of up to 1 m/s [311, 210]) adaptations allow them to forage under extremely high temperatures (up to 60-65°C). This tolerance to heat characterizes the basis of their ecological niche: they wander through their desertic environments in search of dead arthropods that succumbed to the scorching hot conditions [158, 310]. They are central-place foragers: for their food search expeditions, these ants cover an area of several hundreds of meters around their nest [310] with a convoluted path of more than a kilometre in total length [22, 122], always finally returning to their nest. They do so completely on their own, using a range of elaborate navigational strategies (which I will state in this introduction). For all the aforementioned reasons, they have become a model species of insect navigation.

Studying how desert ants solve the complex challenge of travelling through their harsh environment is a fascinating endeavour in itself but is also a step forward in our quest of understanding how brains produce behaviour in general. And, owing to the ranges of distances at which they move and their relatively short lifespans, scientists are able to track them directly on the field, across ecologically relevant contexts, which represents a non-negligible practical advantage.

0.1 Complexity meets modularity

The navigational behaviours displayed by ants must be considered as the result of multiple interactions between what happens inside their brain, what happens in their surrounding environment and everything that happens in between. Sensory perception, which depends on the individual's position in the environment, generates integrative processes in the brain which drive action, which in turn alters the perception of sensory organs – all in a completely closed loop of interactions.

Jakob von Uexküll's concept of Umwelt [297] describes the personal way of seeing the world that each individual has: an active experience resulting from its own specific sensory filters and motor systems. As highlighted by this view, understanding the mechanisms of navigation implies to consider the ants' Umwelt and the natural environment they inhabit [81, 332].

Such an approach (which can be defined as 'bottom-up') has been behind the strong naturalistic background of insect navigation research for more than a century. Clever experiments using ants, bees and wasps allowed early naturalists to unravel some of the apparent mysteries of the insects' remarkable abilities. Fabre, for example, observed that

honeybees that he had displaced for several kilometres were readily able to return to their hive [65]. Santschi showed, for instance, that ants could use the sun as a compass cue when wandering through the desert [236]. Cornetz [49] looked at these ants' paths and described their "*Ligne d'équilibre*", the "*absolute internal sense of direction*" linking them to their nest. An ever-growing field of research has followed since, with some iconic experiments in the mid 20th century. Tinbergen's experiment with a solitary wasp (*Philanthus triangulum*) using a circular landmarks array to pinpoint its nest [286], von Frisch's first description of honeybees communicating to nest mates the location of interesting food sources through the so-called waggle dance [296] or Wehner and Rüber [307] who identified that desert ants – and Cartwright and Collett [29] with bees – could use an egocentric view-matching process in order to reach their nest visually.

What these early studies already pointed at, and which became central in our understanding of navigational behaviours, is the so-called 'navigational toolkit' [312]: an ensemble of rather simple 'behavioural modules' that can act to some extent independently of each other but also complementarily when interacting together. This could well be the result of natural selection: layers and layers of history of whatever worked best in a particular ecological niche. Many independent modules might therefore have evolved separately in a 'mosaic way' [309], allowing new interactions to appear, which ultimately gave rise to the specialised complex behaviours observable today.

In this introduction, I first state an overview of the different behavioural modules composing the classic navigational toolkit outlined by Wehner [312] – albeit with slight additions. Once the behavioural modules have been presented, I take another approach by presenting what is known about the neural hardware and how it may account for navigation-related computations. Then, I argue that linking behaviour to neural hardware is not trivial and that relying on theoretical models is a useful and essential step to achieve this link.

0.2 The navigational toolkit in light of behaviour

0.2.1 Vector-based navigation

Among the very first recorded experiments with desert ants was one by Piéron [214]. He noticed that individually foraging ants attempting to return to their nest were able to walk straight back there even after a very convoluted outward journey. When he displaced them, he saw that the ants kept walking in the same straight fashion, parallel to the nest-ward path they followed before the displacement, and for distances equivalent to where their nest should have been had they not been displaced. This now classic

displacement experiment has since been reproduced in several different paradigms and with many arthropod species [112, 15, 59, 133, 316, 44, 203, 296].

This described homing behaviour has been termed as *Path Integration* [170]. At least two basic components are needed to achieve Path Integration, namely, the need of directional and distance information. These two sources of information are theoretically sufficient to allow an agent (animal, robot) to monitor its movement in space at all times and update a representation in working memory of its total displacement; with the starting point as reference. Thus, the total displacement vector that has thus been built-up along the travel can then be used to go back to the origin of the journey.

Indeed, desert ants (as other homing insects) may do so using a combination of external and idiothetic cues. The principal compass direction (angular reference) comes from the sky: the polarization pattern of the sky light, the position of celestial bodies (the sun, moon, or the milky way depending on if the species is diurnal or nocturnal) and the spectral gradient of light [101, 104, 19, 231, 303, 335, 64]. For distance estimation, ants rely predominantly on a stride counter [324] but detection of optic-flow [229] is also used.

Path Integration is thus quite useful for homing and is most easily read out by displacing an insect attempting to do so. But there are other examples of vector-based navigation which may or may not be directly considered Path Integration. For instance, honeybees are able to transfer to their nestmates the location of important feeding sites through the famous ‘waggle dance’ [296]. They do so by communicating the distance and directional components, which is essentially another readout of the vector between the hive and the feeding site – with one critical difference being that the communicated vector is reversed compared to the homeward path integration vector. Whether these two vectors are encoded in the same memory is however still unclear. Similarly, ants and bees are also known to be able to return to feeding sites that they already visited, using such ‘inversed’ Path Integration vector [296, 219, 40, 311, 318, 316] (see chapter 1 for a potential implementation of such memories). Another example of vector-based strategies lies in the observations of bees able to take novel shortcuts between known food locations [161]. This process has been suggested to be the result of vector addition [50]. The model presented in chapter 1 of this thesis suggests how to conciliate many of these vector-based strategies with neural hardware.

The compass component of the Path Integrator is known to be influenced by idiothetic cues as well: bumblebees are known to modulate the angle of their displacement during homing to accommodate for strong winds using optic flow [225] and ants have been shown to use proprioceptive information to detect wind direction, which can in turn be used as a ‘wind compass’ [325, 188, 329].

Even if the allothetic nature of the compass information helps mitigate occurring errors, Path Integration is still a process that is prone to drift and error accumulation. It thus becomes less accurate as the distance from the origin increases [166]. Fortunately, ants can compensate for it by also taking advantage of the terrestrial cues they perceive visually while roaming through their environment.

0.2.2 Use of visual terrestrial cues

Visual information can be used by navigating insects and, in fact, represents often a major source of guidance. For instance, long-range migrators, such as the monarch butterfly (*Danaus plexippus*), despite mostly relying on sky compass information, have been observed to visually follow salient ground structures [183]. Insects navigating on the ground have at their disposal a wide range of visual terrestrial information, especially in more cluttered terrains.

One relatively simple visual navigation technique that social Hymenoptera such as ants, bees and wasps use is beacon-following: aiming at a conspicuous cue near the nest, visible from afar [41, 42, 87]. But the visual strategy that is generally assumed is the matching of views learnt ‘en route’ (i.e., not mere beacon-following). It was originally assumed, in some early behavioural experiments, that this view-matching process was based on the use of prominent ‘landmarks’ identified along the way [307, 286, 29]. However, it was later revealed that insects might not rely on individually identified landmarks, but rather on the whole panorama [47, 213, 84, 328, 150, 196, 248]. Of these whole panoramic images, the shape of the skyline seems to represent an especially important cue [74, 306, 84, 85, 141, 213, 273, 245]. Ants are thus capable of reaching their nest from locations they never experienced before, as long as these locations are within a specific radius around the nest. Yet, they are not able to do so when the views are obstructed [196, 331]. Also demonstrating the use of views to navigate, and perhaps even more convincingly, is the fact that ants are able to learn and follow their own idiosyncratic routes to and from food sources [331, 330]. They are able to recognize and recapitulate these routes from any point along them, only using vision [140, 155, 330].

What we know about view-based navigation comes from the combination of behavioural observations, the description of the sensory organs, modelling studies, and the reconstruction of what insects may actually see [246, 328, 196, 190, 213, 60, 281]. As reviewed by Möller and Vardy [178], models of visual navigation are numerous, owing to their common interest to neuroscientists and roboticists, and this introduction is not aiming to list them all. But some main ideas are worth mentioning because they highlight the two main questions concerning visual navigation: ‘*How are the views encoded?*’ and ‘*How are they used to guide behaviour?*’

0.2.2.1 How are the views encoded?

Let's for instance consider the classic 'snapshot' model [307, 29], which is one of the first strategies proposed for visual navigation in insects. This model postulates that, by extracting landmarks from the current view and from a memorised reference view, the direction yielding the smallest retinal discrepancy between these landmarks (in position and apparent size) should be selected. Regarding the first question of how the views may be encoded, extracting landmarks from the visual surroundings makes the most sense to us humans since we are able to assign semantic labels to the extracted elements but for ants, considering the visual surroundings as a whole could instead be the more sensible and parsimonious approach. Indeed, analyses based on optic flow [290] or pixel-wise image differences [344] show that feature extraction is actually not necessary. While it seems that insects are still able to respond to individual landmarks [43, 25], this may simply be due to the salience of these objects within their panoramic view [342]. What mostly stands out is the importance of the wide visual field (panoramic-like) and the low-resolution characteristics of ants eyes [249], which essentially act as low-pass filters for the visual information, eliminating noise and preventing overfitting details [168, 334]. Other hypotheses have been proposed for the encoding of the views, often focused on reducing the dimensionality of the information to be stored: for instance, one-dimensional vectors of the horizon height [75, 179] or luminance intensity [94], the average of multiple landmark bearings [176, 144] or optic-flow vectors [290].

The common outcome across many models of insect visual navigation is that the visual information does not necessarily need to be kept retinotopic as long as it stays egocentric. In other words, encountering a view that was seen before (from the same vantage point) should be sufficient to recover guidance information. But what about when the insect faces a different direction, one that it has not experienced before? This is of special interest for our second question of '*How are the views used for navigation?*'.

0.2.2.2 How are the views used for navigation?

One possibility is, when the current view is unknown, to sample the environment until a familiar view is encountered and matched. Zeil, Hofmann and Chahl [344] demonstrated that panoramic views of natural scenes vary in a smooth and regular fashion: by taking regularly spaced panoramic snapshots and comparing the pixel-wise root mean square difference between these snapshots with a reference, the resulting *translational image difference function* (tIDF) constitutes a smooth 3-dimensional gradient with its minimum at the reference location. Thus, assuming that the animals can obtain such measure of difference from the view at any location, a gradient-descent technique could be used for successful navigation [213]. In addition, albeit varying less smoothly than a tIDF, the

root mean square difference determined by rotating a panoramic snapshot relative to a reference orientation – *rotational image difference function* (rIDF), has a minimum at the reference orientation. The rIDF minimum is robust to a good amount of positional error as it can be detected from a certain distance as long as the orientation is the ‘correct’ one.

This ‘visual compass’ [344, 290] could therefore be sufficient for the insect to recover directions from novel places only by *alignment matching* (i.e., recovering the direction in which the reference view was memorised, even with some degree of positional discrepancy). Thus, having acquired reference views from a few orientations around the goal [83] should allow homing [10, 338, 54, 272, 212]. Sampling multiple directions can be achieved for instance by stopping at places and scanning all directions [339, 341] or even while moving by oscillating regularly between left and right turns [139, 97] – two mechanisms actually displayed by navigating insects in unfamiliar environments [86, 339, 191, 341]. However, rIDF- and tIDF-based models cannot capture all navigational behaviours displayed by ants (see for instance [331]). Also, such pixel-wise difference methods assume that the views are memorised retinotopically, which is likely not the case in the insect brain. An alternative solution is the familiarity-based encoding of the views.

0.2.2.3 Conciliating encoding and guidance: familiarity-based models

Memorising multiple unprocessed panoramic snapshots and being able to mentally compare the current view to this memory bank is relatively cheap computationally speaking. However, being computationally cheap does not necessarily mean that the neural implementation is parsimonious [5, 163].

An alternative approach, also computationally cheap but more bio-plausible, has been proposed [5, 185]. Instead of being stored as multiple individually identified, ordered snapshots, the views can be stored into one common holistic memory, losing all positional or directional information [11, 10, 5]. The comparison of the current view with the holistic memory containing all the familiar views is not indicative of ‘where you are’ nor ‘where to go next’, it is only informative about whether the current view has been seen before or not. It thus directly reflects a rating of the apparent ‘familiarity’ of the current view (and much like the reduced dimensionality evoked above, this encoding is a one-dimensional parameterization of the view). Such models fit with real behavioural data where ants are able to orient using panoramic views previously acquired from a different location [e.g., 76, 196]. Moreover, the circuitry of the insect brain appears to be readily able to bear such encoding (see below, **Mushroom Bodies** section).

Yet, these familiarity-based models are still not the definitive answer to capture all

observed visually guided behaviour. For instance, it was recently suggested [252] that the sequence of how views were learnt may actually have an influence on the perceived familiarity during visual route-following, which contrasts with the idea of a non-labelled, non-ordered holistic encoding. Models presented in chapter 3 and chapter 4 tackle the problem of a holistic encoding of views and the use of familiarity for guidance, in regard with neural hardware.

0.2.3 Learning walks & flights

Learning walks/flights are a form of active sampling of the surroundings of a goal: typically the nest [reviewed in 343]. They are more a well-defined behavioural routine with a very stereotypical and likely hardcoded choreography rather than a complex behaviour per se and are usually not explicitly included as a part of the classic toolkit description [312]. However, their ontogeny is modulated by the positional uncertainty [339], as well as by the individual's experience [70, 126, 343]. For these reasons, and because of their critical importance in the establishment of other behaviours – such as visual goal pinpointing (see below), I chose to include them here.

Ants, bees and wasps are systematically seen to perform learning walks/flights [46, 232]. Learning walks/flights typically happen at the onset of these insects' foraging life, where the adults leave their role as nurses and nest-confined workers [314] and start venturing outside searching for food. This interior-exterior transition [232] is crucial, and it is then that the new foragers typically spend 2 to 3 days [70, 126] performing very stereotyped sequences of movements around the nest entrance, gathering the necessary visual memories they will later use for visual homing [199, 313, 192, 269, 70, 71, 72, 89, 46, 126, 280, 187]. In general, learning walks and flights are all organised similarly: the insects perform loops around the goal, of increasing distance and covering all directions around it. Importantly, they regularly look back towards the goal, supposedly to acquire the important goal-centred panoramic views [46, 187, 109].

In order to be able to perform learning walks/flights, these insects likely rely on information derived from their path integrator state [83, 187, 70, 71, 72, 46, 126].

It should seem plausible to consider that the encoding of views for route-following and views for reaching a goal could result from the same mechanism [342]. Indeed, models storing a set of views around the goal as well as views along the route are able to capture both the idiosyncratic route-following behaviour [331, 328] and homing from unfamiliar locations [196, 83, 282]. In this form of encoding, the best correspondence between the current view and all learnt views occurs naturally when aligned with the nearest learnt view, in one go (that is, without the need to identify beforehand which of all learnt views

is the nearest one). Thus, acquiring egocentric views through learning walks which are pointing towards the goal from different vantage points seems to be sufficient to extend the visual route following abilities into visual goal pinpointing abilities [10, 338, 299, 342].

Learning walks are thus a learning routine that allows foragers to acquire important information about the nest surroundings that should stay relevant for their whole life but cannot be genetically encoded (as the nest location is stable for an individual, but not across generations [46]). In addition, experienced individuals still perform learning walks, either around new important feeding sites or when encountering unexpected novelty in the visual surroundings of locations they already know [126, 232, 187, 339]. Overall, by being linked to vector-based computations while also allowing specific view-based abilities to emerge, learning walks can be considered as an important computational component. The model in chapter 4 of this thesis demonstrates how a well-defined learning walk strategy can improve visual navigation in a complex environment.

0.2.4 Systematic Search

Another example of stereotyped routine for active sampling is the *Systematic Search* behaviour. The systematic search, unlike learning walks, is included in the original toolkit [312]. It possesses several similar characteristics to the ones described for learning walks and can thus be included here and considered as a behavioural routine, too.

The overall organisation of the systematic search can be described (not without recalling the Learning Walks organisation) as a series of loops of increasing size, centred on the starting location and slowly covering all angles around it [315]. In other words, it also likely depends on the underlying Path Integrator [244]. Most often, this search routine is employed as a backup strategy when no other information is available or when the other guidance mechanisms become unreliable. For instance, when the internal vector is in the ‘zero-vector’ state, but the visual surroundings do not provide enough guidance information [315, 186, 243]. Also, there are examples of systematic searches being used for locating food sources by ants [326, 242] or when bees use a vector memory communicated by a hive mate by waggle dances [218, 224].

What is especially interesting here, is the fact that the spread of the search appears to be correlated with the estimated positional uncertainty: the higher the positional uncertainty, the larger the spread [164, 243, 246]. As we said before, because the Path Integrator uses egocentric cues and is a process that accumulates errors, it means that the longer the foraging trip is, the larger the spread of the search will be [165]. Systematic search is also used in response to visual changes of the expected terrestrial cues during homing [197] or directly in correlation with the degree of visual complexity in

the surroundings of the insect [34, 246, 337]. An interaction between the roles of Path Integration uncertainty and terrestrial cues can also be seen in bees, which display a search spread that is dependent on flown distance, but which is reduced if they encounter familiar views en route [261].

The systematic search routine is thus influenced by both vector-based and view-based experience, and even more importantly, triggering the systematic search might not be under the control of an explicit motivational change: it could emerge as a by-product of the accumulated uncertainty of the Path Integrator. The computational model of Path Integration in Stone et al. [271] indeed shows that a systematic search behaviour emerges from the Path Integrator oscillating around its zero-vector state; such emerging properties are demonstrated in models in chapter 1 and chapter 4, and discussed in chapter 5.

0.2.5 A complex and distributed integration

There is probably no explicit switch between the use of the navigational modules, neither in time nor in space. For example, modules like the Path Integrator seem to be running continuously, any time the ant leaves the nest. The final guidance output appears to be the result of an integration, weighting the role of each independent module according to their apparent certainty [333]. But the different modules likely interact in more ways than just through simple potentiation of their respective motor outputs. For instance, vector information from the Path Integrator could be integrated with visual memories [50, 45] or be used as a cue to trigger learning during learning walks [187].

In fact, the Path Integrator state seems to act as more than just a navigational tool: it often acts as an internal effector controlling a wide range of behaviours and motivational states. It has been shown to modulate the aggressiveness towards conspecifics [138], as well as the attractiveness of nest-like odours [21], which both require potentiation around an individual's real nest (i.e., the centre of its own world), but not around other competing nests. Many other elemental motivational states have been shown to be influenced by the Path Integrator state, such as sleep and arousal [289, 56] or the overall speed of movement [20] for example.

We talk here about behavioural modules in the sense of elementary observable navigational strategies displayed by insects. But one given navigational strategy could emerge from interactions between completely different 'computations' in the brain. Likewise, different neural substrates and brain areas may be used by the same computational module but for two very different behavioural modules (note that the 'computations' are not necessarily how information is 'mentally represented'). As human observers, we can only separate and classify the observed behavioural modules along our own limited bias. Beha-

vioural descriptions being low-dimensional and limited by human language [3] have been a recurrent problem in ethology since the very first ethograms. As a consequence, even if labelling the behavioural modules of navigation the way we did certainly helped our global understanding, it is important to keep in mind that the reality of what happens in the insect brain is probably not as clear cut. All the modules run in parallel, and all kinds of deep interactions likely happen constantly between them [217, 148, 333, 113]. Considering these non-linear interactions and the fact that several sensory modalities can input into a same brain area, the notion of ‘behavioural modules’ starts to show its limits. We are faced with a multi-level problem, as there appears to be no direct one-to-one mapping between brain modules and behaviour. In this thesis, I tried to clarify this problem with chapter 5. We may thus here revise the navigational toolkit in light of the knowledge brought by neurobiology.

0.3 The navigational toolkit in light of neurobiology

The recent progress of neuroscience, with tools allowing to identify and trace networks down to individual neurons, made it realistic to try and relate behaviour to actual neural circuitry. Looking at the hardware level has thus provided scientists valuable insights about which brain areas may be involved in specific computations. However, the way that these computations actually relate to behaviour is not so straightforward. More precisely, interspecific comparisons revealed that, even if the behavioural repertoire is very diverse across species, the neural hardware in the integrative areas is mostly conserved in insects. The *Central Complex* and the *Mushroom Bodies* represent two of the most studied structures in the insect brain and seem to assume key roles in a number of navigational behaviours. In this thesis, I will present modelling efforts for each of these structures in chapter 1, chapter 3 and chapter 4.

0.3.1 The Central Complex: Home of the vector-based navigation?

The *Central Complex* (CX) [117] is a group of neuropils located in the central brain of all insects. Depending on the species, it consists in general of 4 to 5 subunits: the *Protocerebral Bridge* (PB), the *Central Body* which is itself separated into the *Upper* (CBU) and *Lower* (CBL) units, and the *Noduli* (NO). A columnar structure is found in the PB, CBU and CBL, with a very distinct neuronal architecture of generally 8 to 16 vertical slices [321]. This columnar and horizontal architecture has been identified in flies [215, 274, 96], beetles [302] and locusts [321, 189]; but the finer details of its organization were revealed in the desert locust (*Schistocerca gregaria*) through neuroanatomical studies

[100, 102] that focused principally on polarized light responding neurons. Polarized light perception had already been demonstrated early in ants [304, 58] and bees [295] but only behaviourally. In fact, the pattern of polarized light composes, together with the position of the sun, a very robust external reference frame in the diurnal sky. Thus, it appears sensible to think that insects had evolved efficient neuronal processing of it (e.g., for vector-based navigation). What is most interesting in all the comparisons across species, is the fact that the highly conserved architecture of the CX does not only accommodate for polarization vision but also for a range of other sensory modalities: mechano-sensory inputs (cockroaches, locusts) [227, 114]; olfactory cues (bees) [116]; optic flow (flies, cockroach) [319, 130]; movement (locust) [16, 230]; visual information (drosophila, dung beetles) [253, 64]; idiothetic cues (drosophila, cockroach) [254, 134, 291]; wind direction (drosophila) [201].

Other important neuroanatomical studies of the CX were conducted on *Drosophila melanogaster*, including real-time recording of populations of neurons [254, 88, 288, 135]. These studies helped confirming that the role of the CX was likely to encode the insects' current heading direction, and to compare the current with a desired heading direction [216, 123]. Interestingly, there is evidence that multiple compasses may be integrated in the CX [206], likely to provide a holonomic representation of the current direction [153, 154]. Thus, global and local reference frames could easily be integrated in the CX compass signals [98].

Giraldo et al. [79] showed that flies are able to orient with reference to a sun cue and retain this orientation for several hours, but not for days. This is in accordance with their ecological needs and in opposition to migratory monarch butterflies which can follow a compass direction over days. What this especially shows is that sensory systems are often sufficient to account for a great deal of behavioural variability. This is likely due to how they have evolved in response to the unique problems posed by the environment the animal inhabits [308]. Thus, the 'matched filter' for the sun position that monarch butterflies have evolved may be sufficient to explain the huge behavioural difference in sun-related orientation in these two species, and the CX architecture itself is flexible enough to encode the current heading in a reference-agnostic way.

The described connectivity in the Central Complex, with the columns of direction-specific cells and speed accumulation cells is very much reminiscent of a Cartesian projection of the vector components over multiple axes [101, 7, 80, 93, 132, 271, 103, 117]. The efficiency of a Cartesian projection had actually been suggested before in insect navigation [171], including the added reliability provided by axes redundancy [292]. The functional organisation in the CBU and even its topological toroid-shaped organisation in *Drosophila* is reminiscent of a polar projection, with its bump of activity reflecting the insect's current orientation at all times.

There has been strong evidence of the CX' implication in motor control [211]. *Drosophila* mutants of the CX show deficits in walking coordination and turning ability during walking and flight [12, 278, 124, 277]; lesions in the CX caused deficits in turning ability in cockroaches [223, 99, 228], whereas extracellular recordings of neurons in the CX could predict upcoming turns [159].

One major pre-motor area is considered to be the *Lateral Accessory Lobes* (LALs) [256, 28, 267]. The LALs are paired neuropils surrounding the CX. They appear to be well conserved across many arthropod species [275, 285, 267]. The LALs receive direct input from the Optic Lobes and Anterior Optic Tubercles [193, 102], from the olfactory pathways [169] and higher processing centres including the Mushroom Bodies [8, 193], and are upstream of the thoracic motor centres. Behaviourally, they show implications in both small-scale searching behaviours and long-range goal-directed navigation. For instance, they have been shown to play a key role in zig-zagging behaviour for pheromone tracking in *Bombyx mori* silkmoths [129]. Such oscillating behaviours have also been seen in walking and searching ants [339, 337, 315] and wasps [280], among others. The inputs to the LALs are principally ipsilateral [204], but some contralateral visual and olfactory inputs have also been shown [195, 194]. The appendix appendix B explores this lateralisation of the information in the insect brain.

In short, the CX is a prime example of the optimization and the modularity encountered in the insect brain. It functions as a general-purpose compass, able to equally represent local or global reference frames and is implicated in motor commands. This suggests it is not only the siege of path integration, but many vector-based (and potentially other) strategies. It is very likely one of the most conserved computational modules and it features a broad range of adaptations to various sensory input, as well as differences in its motor outputs [237], which might account for a number of different navigational strategies observed across species. Chapter 1 presents a modelling study that links several complex vector-based navigational strategies to the Central Complex circuitry.

0.3.2 The Mushroom Bodies: where familiarity-based navigation becomes possible?

Another well-studied region of the insect brain are the *Mushroom Bodies* (MB) neuropils. This is a higher-order brain centre [162] is composed of two large structures shaped like mushrooms (hence their name), that are extremely well conserved across species. They have been described in ants, wasps, locusts, crickets, and in more depth in *Drosophila*, honeybees, and cockroaches [106, 107, 276, 340]. Most of the focus of the studies regarding the MBs has been geared towards olfaction, probably because of the very prominent olfactory inputs that the MBs receive, as this sensory modality is very prominent in a

number of species. It has also been shown that the MBs were involved in associative learning [162, 106]. The organization of the olfactory pathways to the MBs follow a fan-out/fan-in architecture. Axons of the projection neurons (PNs) project from the Antennal Lobes (the first olfactory relay) over to a large pool of Kenyon Cells (the neurons intrinsic to the MBs), which themselves converge onto a smaller set of Output Neurons (MBONs). This architecture, providing both pattern separation and selection, is a schema that has shown to be particularly suited to achieve learning paradigms in artificial neural networks [175, 185, 31, 268].

In fact, these structures are often considered as the main centre for processing high-order information of most modalities, including vision [61] and navigation-related memories [254, 53]. The visual inputs to the MBs are greater in navigating Hymenoptera than in other insects [5, 67], and we now have quite detailed neuroanatomical data in several species regarding the visual pathways reaching the MBs [151, 92].

Structural lesions and pharmacological interventions in the MBs result in defective visual navigation in several species [172, 24, 128]. There are structural changes in the MBs linked to exposure to light in *Cataglyphis* ants and honeybees [66, 270, 269, 240, 184]. These changes include the elimination of non-essential synaptic boutons in the MBs input region and an increase in KCs dendrites in the visual input area [143, 184, 26]. Ultrastructural analyses in the honeybee demonstrated that the combination of these two phenomena enhanced the synaptic divergence of the PNs-to-KCs fan-out pattern [233, 232]. These changes in the visual processing pathways are thus likely a preparation for the new foraging life.

After the pattern-separation happening in the KC layer, the output of the MBs is mapped to sets of differently-valenced MBONs. The balance between these MBONs governs general attraction and avoidance responses, ultimately driving behaviour [8, 111, 202, 208].

Taken together, even if most of what is known of the MBs comes from olfactory learning, everything seems to indicate an important role of this structure for the use of views in navigation. Most strikingly, the architecture of the MBs proved to be a sound substrate for the ‘familiarity-based’ encoding suggested by models inspired by insect behaviour. This familiarity encoding is however not necessarily limited to vision [299] and can include odour [23] and wind cues [325] as well as potentially vector information from the CX. In chapter 3, I explore how the Mushroom Bodies circuitry can accommodate for encoding the views of long routes in a complex environment and how it can provide guidance.

0.4 Outline of the thesis / The importance of modelling in Insect Navigation

As mentioned above, the advances that allowed scientists to trace, record, and manipulate neurons at an increasingly large scale and precision allowed us to gain invaluable knowledge about the circuits underpinning complex behaviour. However, direct links and causal relationships from the neural hardware to the behaviour are often only part of the answer or not sufficient to reach a true understanding of the intricate dynamics at play. For this, a theoretical framework is necessary [232]. The best way to formulate those hypotheses is using models and computational simulations, and insect navigation has been benefitting from these model hypotheses for a long time.

This thesis therefore presents several computational models that will hopefully help consolidating our general understanding of the mechanisms underlying insect navigation.

All the computational models presented here have as common ground that they are strictly constrained by known (or at least plausible) biological connectivity. Similarly, the focus is on their ability to accurately replicate observed behavioural signatures rather than on their absolute, practical performance. Having biological constraints at both ends of the spectrum (known neural circuitry on one hand, and described behavioural signatures on the other hand), these modelling efforts can lead to an actual mechanistical understanding of how behaviour can emerge from the brain in closed loop with the environment. They also generate predictions for both the neuroanatomical and behavioural levels, which can hopefully be experimentally verified. I thus used such a computational approach of modelling, to unravel the link between brain and behaviour, and to develop computational and methodological tools to help other future efforts do so.

0.4.1 Chapters outline

Chapter 1 / The central complex as a potential substrate for vector based navigation

This chapter focuses vector-based navigational strategies and the potential implications of the Central Complex in these behavioural signatures. Stone et al. [271] presented a model that is able to achieve path integration, only using known connectivity of the insect Central Complex. Arguing that insects can also store and use vector memories for several other behaviours, we present an addition to the original model with only minor, biologically plausible changes that can allow the virtual agent to reproduce multiple vector-based strategies: storing and recalling vector memories to return to food sources, take novel shortcuts, perform systematic searches at the feeder and re-calibrate their

vector memories with experience. This model thus suggests how the central complex circuitry is suited to allow for a rich vector-based navigational repertoire.

Chapter 2 / InsectVisionSimulator: an interface for visual navigation models in Python

In this methods paper, we present an open-source library that provides an all-in-one tool for generating 3D simulations of complex insect environments in real time. The tool provides an OpenGL-based rendering engine, a model of the faceted insect eye, as well as a simple agent-based model, which together composes all the groundwork and an easy interface for the modelling of insect 3D navigation in Python. Therefore, this tool enables novel investigations regarding modelling and the interaction with the corresponding navigational behaviour in ants. The question of how these views can be encoded is the topic of the next chapter.

Chapter 3 / Visual pre-processing to facilitate the encoding of views in an insect Mushroom Bodies model

Chapter 3 investigates how views of the complex environment can be encoded in the Mushroom Bodies as well as the importance of several visual pre-processing steps on this encoding. We now know the neural tracts conveying visual information towards the central insect brain areas, notably from the Optic Lobes (OL) to the Mushroom Bodies (MB). There, hypotheses about the encoding of view memories are largely inspired from what is known of the encoding of olfactory information [106]. The exact nature of the different types of processing happening along the several relays before the MBs is still unclear and how these processing steps could actually serve (or harm) navigation is entirely unknown. We therefore present a computational model of the MBs, embedded in an agent moving through the 3D world, using the tool presented in chapter 2. The model focuses on how some known types of visual pre-processing may act on and shape the information before arriving to the MBs, and how the set of parameters chosen in the sparse encoding in the MBs reflects what is observed in real insects.

Chapter 4 / Opponent processes in visual memories: A model of attraction and repulsion in navigating insects' mushroom bodies

While the previous chapter is dedicated to 'how views can be encoded', we here investigate how, once encoded and memorised, these views can be used to generate a navigational behaviour. In order to achieve visual goal pinpointing, it is believed that ants and bees need to memorise egocentric views only when their body is precisely oriented towards the goal. Later on, they are supposed to be attracted by the direction that represents the highest visual familiarity. We show in this chapter, with a computational approach, that this strategy suffers from a major weakness: a single view, taken by itself, does not provide enough information for the insect to decide if it should turn or keep its current movement direction. However, a surprisingly robust solution to this problem arises if,

in addition to attractive goal-oriented views, we assume that repulsive anti-goal-oriented views are also memorised. This hypothesis helps clarify several observed behaviours that were difficult to explain with previous models.

Chapter 5 / Towards a multi-level understanding in insect navigation

This chapter presents an opinion paper which can be considered as part of this thesis discussion. Based on the insights presented in the previous chapter of this thesis, this review highlights the multi-level nature of research in neuroethology: how neural circuits can produce complex behaviours is not straightforward, and in order to reach a true understanding of the interactions it is necessary to formulate functional hypotheses of the transitions between levels. We argue that the field of insect navigation has been benefitting from a two-sided approach with both behavioural and neurobiological studies and that it is a perfect application of the interest of modelling.

0.4.2 Appendices outline

Appendix A / The role of attractive and repellent scene memories in ant homing (*Myrmecia croslandi*)

An adaptation of the model of integration of attractive and repulsive visual memories (chapter 4) predicts that ants placed in a completely unfamiliar environment should behave similarly to when they are at the nest. This prediction is confirmed behaviourally with *Myrmecia croslandi* ants.

Appendix B / A lateralised design for the interaction of visual memories and heading representations in navigating ants

We combine behavioural experiments with a computational model implementing robust navigation in a two-stage process involving both the CX and the MB. Interestingly, the results suggest a lateralised design, where left/right turn signals are segregated in the right/left hemispheres.

Appendix C / A killjoy perspective on object representation by bumblebees

In response to Solvi, Al-Khudhairi and Chittka [258], suggesting that bumblebees trained to discriminate objects by touch could distinguish them through vision (and vice versa) thanks to a cross-modal representation, we argue that this behavioural feat may be explained by egocentric heuristics rather than an abstract representation of object shapes. We call for more considerations of the animals' ecology, neural circuitry and actual behaviours.

Chapter 1

The central complex as a potential substrate for vector based navigation

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The Central Complex as a Potential Substrate for Vector Based Navigation

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Insects use path integration (PI) to maintain a home vector, but can also store and recall vector-memories that take them from home to a food location, and even allow them to take novel shortcuts between food locations. The neural circuit of the Central Complex (a brain area that receives compass and optic flow information) forms a plausible substrate for these behaviors. A recent model, grounded in neurophysiological and neuroanatomical data, can account for PI during outbound exploratory routes and the control of steering to return home. Here, we show that minor, hypothetical but neurally plausible, extensions of this model can additionally explain how insects could store and recall PI vectors to follow food-ward paths, take shortcuts, search at the feeder and re-calibrate their vector-memories with experience. In addition, a simple assumption about how one of multiple vector-memories might be chosen at any point in time can produce the development and maintenance of efficient routes between multiple locations, as observed in bees. The central complex circuitry is therefore well-suited to allow for a rich vector-based navigational repertoire.

Keywords: vector, path integration, memory, insect, navigation, neural modeling, traplining, central complex

1. INTRODUCTION

It is well established that central place foraging insects, such as bees and ants, keep track of their displacement when they venture outside their nest by a process called path integration (PI) (Collett and Collett, 2000a,b). By combining compass and speed information, they continuously update a home vector that allows for a direct return to their nest after arbitrary outward routes (Müller and Wehner, 1988; Collett and Collett, 2000b). However, insects do not use their PI system only for homing. For instance, they can also store PI vector-memories and use them to return to a known food location (Wehner et al., 1983; Collett et al., 1999; Wolf and Wehner, 2000), and take shortcuts between multiple food locations (Menzel et al., 2005).

A recently published neural model (Stone et al., 2017) closely follows the connectivity of the insect Central Complex neuropil (CX) and uses properties of identified neurons in this circuit that respond to polarized light compass information and optic flow information to integrate an

outbound path. In this model, the home vector, at any point in time, is assumed to exist as a distributed sinusoidal activity pattern across two sets of 8 columns, where the phase indicates direction, and amplitude indicates distance. The model also provides a mechanism for using such a PI memory to drive the animal directly back home. Offset connections between columns produce a comparison of the current heading to the home vector direction, and indicate whether steering left or right would improve the alignment. As the circuit continues to integrate movement, the home vector amplitude will decrease as it approaches the home position. When it becomes zero, an emergent search behavior will result, unless there is a mechanism to recognize home. The model accounts for changing travel speed and is also robust to decoupling between the agent body axis and direction of movement (Stone et al., 2017), something that bees (Riley et al., 1999), wasps (Stürzl et al., 2016) and ants (Pfeffer and Wittlinger, 2016; Collett et al., 2017; Schwarz et al., 2017) can do.

The steering mechanism in this model is generalizable beyond the use of a home vector. Different sources of information about the “desired” heading or destination could be switched in, or additively combined onto the steering neurons, and the system will automatically steer to reduce the difference between the current and desired directions. While it is interesting to speculate how this might include information from sources other than PI (e.g., learnt terrestrial cues), here we focus on cases where the alternative activation is derived from a “vector-memory.” That is, we assume that, as in other models (Cruse and Wehner, 2011; Hoinville et al., 2012), the animal can store the current state of its home vector (the neural activation pattern) when it encounters salient places in its environment, and can later recover this vector-memory to guide future behavior (Figure 1A). We suggest some simple (hypothetical) neural circuitry that would add this capability to the CX model (Figure 1B) (we assess its biological plausibility in the discussion) and show it can support several interesting phenomena observed in insect navigation.

Memory-directed movement: Insects that have found a food source on a previous excursion can return to it on a direct route. It is assumed this involves storage of a memory of the PI state when the food was reached (Wehner et al., 1983; Collett et al., 1999; Wolf and Wehner, 2000). We hypothesize that such a memory could be integrated as a simple inhibitory influence in the CX steering circuit to produce food-ward steering and search around the food location (Figures 2, 3).

Vector-memory re-calibration: Insects experiencing a PI inconsistency when returning from food to the nest due to a forced displacement, appear to make a partial adjustment of their memory of the food location (Collett et al., 1999; Wehner et al., 2002; Bolek et al., 2012) (although the extent of this “re-calibration” seems to vary with experimental conditions). We suggest how this updating of a food-ward vector-memory could occur (Figure 4).

Shortcutting: Bees have been observed to make novel shortcuts between remembered food locations (Menzel et al., 2005). It has previously been demonstrated that this can be obtained by vector addition, i.e., combining the current state of the home vector (from an arbitrary location such as a first food source) with a

vector-memory from home to another food source (Cruse and Wehner, 2011). This produces a vector directly from the current location to the food. We show that such shortcutting would be a straightforward consequence of switching between memories in the CX circuit; importantly, this demonstrates how vector addition could be implemented in the insect brain (Figure 5).

Multi-location routes: Bees often feed on multiple locations (e.g., feeders or flowers patches) before returning home, and have been shown to take efficient multi-location routes, or “traplines,” that minimize the overall journey distance (Ohashi et al., 2006; Lihoreau et al., 2012b; Buatois and Lihoreau, 2016). We investigate a simple rule by which the neural circuit output can be used to choose the next location to visit, and test whether this produces multi-location routes similar to bees (Figure 6).

Route ontogeny: Finally, we explore how such multi-location routes might develop over repeated foraging excursions through a combination of random exploration and vector-memory recall (Figure 7).

2. METHODS

2.1. Environment and Agent

We simulate (using Python 2.7) an agent moving in a 2D environment. Movement in these simulations is discretised in time and space. Units are therefore arbitrary, and different walking “speeds” may be achieved by changing the length of the spatial step that the agent moves at a time. In the following paper, we describe the agent’s movement as time steps (t), where the “speed” is generally kept constant during tests, but variable during random walks (see **Supplementary Material** section “Random Walks”). The environment typically contains a nest, one or multiple feeders, as well as optional obstacles. The nest and feeders are circular with a small defined radius (relative to the typical environment size) within which the agent is assumed to have “landed” successfully at the target, and a larger radius, or “catchment area” which is assumed to provide an olfactory signal (or other attractive signal) that could steer the agent to the target. Obstacles can have circular, rectangular or wall-like shapes and prevent the agent from passing through the area they occupy (e.g., walls enclosing the agent in an arena) by emitting a very short range repulsion signal that can steer the agent away.

The agent’s size is one spatial unit. It is assumed to have sensory information about its heading direction in an absolute external reference frame, as could be supplied in real insects for example by a celestial compass (over a short time duration, or with internal clock correction, Labhart and Meyer, 2002). It is also assumed to have information about its instantaneous speed of movement in its heading direction as could be supplied by optic flow, step counting, or efference copy. These provide inputs to the CX model for path integration and control of steering. Lastly, the agent is equipped with two “detectors,” oriented at 90 degrees, that provide no input whatsoever to the neural model we describe, but only act as modulators of the agent’s turning intensity in response to “attraction” or “repulsion” signals emitted by objects in the environment such as the nest, feeders, or obstacles.

The agent's starting position for each simulation is (unless specified otherwise) set at the nest. Its position is updated iteratively depending on its speed v and heading θ :

$$\begin{aligned}x_t &= x_{t-1} + v_{t-1} \cos(\theta_{t-1}) \\y_t &= y_{t-1} + v_{t-1} \sin(\theta_{t-1})\end{aligned}\quad (1)$$

The speed and heading can be controlled by a random walk process (see "Random Walk" section in **Supplementary Material**) or have a fixed speed ($v_t = 0.15$) and a heading given by the outputs of the CX steering neurons (see section 2.2), depending on a flag that sets the current motivational state (see below). Or, when an obstacle or a goal is detected, the heading is given as follows:

$$\begin{aligned}M_{left} &\propto (R_{left} A_{obj}) \\M_{right} &\propto (R_{right} A_{obj})\end{aligned}\quad (2)$$

$$\theta = (M_{right} - M_{left}) + noise\quad (3)$$

with M_{left} and M_{right} the modulation for left and right sides, respectively, which are proportional to the left and right readings R_{left} and R_{right} of the two detectors, multiplied by the detected object's attractiveness A_{obj} . The added *noise* is drawn from a VonMises distribution centered on 0:

$$noise \sim VonMises(0, \kappa)\quad (4)$$

where $\kappa = 100.0$ is the concentration of the VonMises distribution. Note that this is considered to be a basic reflex behavior of the agent, which by-passes the CX circuit. Finally, in such case of an environment-driven steering modulation, the agent's speed is also modulated by an increased drag value (multiplied by a factor of 1.5), providing better turns.

2.2. Central Complex Model

For convenience, we provide here an overview of the mathematical description of the CX model, but we deliberately omit the detailed biological justification, which is covered at length in Stone et al. (2017). Layers 1–4 are identical to the previous model. A "vector-memory" neuron has been added, which can store the output state of layer 4, and in turn, modulate this output before it reaches layer 5 (steering).

In overview, the circuit consists of a set of direction cells (layer 3) that divide the azimuthal space and are activated by the current heading of the agent (layers 1 & 2). Mutual inhibition in layer 3 forms a ring attractor circuit creating a stable distributed pattern in the form of a sinusoid. A set of integrator cells (layer 4) receive speed input but are inhibited by their corresponding direction cells and thus accumulate distance traveled opposite to the heading direction, creating a distributed representation of the home vector. The vector-memory allows the current state of the home vector to be stored when the agent is at salient locations (feeders). The state is stored in the synaptic weights of one neuron for each memory location. Homing is controlled by steering cells (layer 5) that compare the integrator cell activation to the current direction cell activation to determine if the animal should turn

left or right. Vector-memory can be used to selectively influence this comparison process.

This circuit uses firing rate model neurons, in which the output firing rate r is a sigmoid function of the input I :

$$r = \frac{1}{(1 + e^{-(aI-b)})}\quad (5)$$

where parameters a and b control the slope and offset of the sigmoid. On this value is added a Gaussian noise $N(0, \sigma_r^2)$, with $\sigma = 0.1$. This output firing rate is, across all layers, subject to a clipping between 0 and 1 to prevent the applied noise to depart from the range $[0, 1]$. The input I is given by the weighted sum of activity of neurons that synapse onto neuron j :

$$I_j = \sum_i W_{ij} r_i\quad (6)$$

The value of the parameters for slope, offset and connection weights for each layer are provided in **Supplementary Material**.

2.2.1. Layer 1 - Speed Input

To implement input to our speed-sensing (TN2) neurons, we simulate forward-to-backward optic flow sensing, taking into account the diagonally offset preferred angles of identified TN-cells in the CX noduli in each hemisphere (Stone et al., 2017):

$$\begin{aligned}I_{TN_L} &= [\cos(\theta + \phi), \sin(\theta + \phi)] \cdot \mathbf{v} \\I_{TN_R} &= [\cos(\theta - \phi), \sin(\theta - \phi)] \cdot \mathbf{v}\end{aligned}\quad (7)$$

where \mathbf{v} is the velocity vector of the agent, \cdot the dot product, $\theta \in [0, 2\pi)$ is the current heading of the agent and ϕ is the preferred angle of a TN-neuron, i.e., the point of expansion of optic flow that evokes the biggest response. For our model, a default preferred angle of $\phi = (\pi/4)$ was used. TN2 neurons have their value clipped between 0 and 1 so that they respond in a positive linearly proportional manner to I_{TN} , but have no response to negative flow (backward motion):

$$r_{TN2} = \min(1, \max(0, I_{TN}))\quad (8)$$

In practice for this paper we assume that the agent is moving in the direction it is facing, i.e., $\mathbf{v} = [\cos(\theta), \sin(\theta)]v$, which will produce an equal response in each TN2 neuron, i.e., $I_{TN_L} = I_{TN_R} = \cos(\phi)v$ regardless of the heading θ .

2.2.2. Layer 1 - Directional Input

The first layer of Directional input consists of 16 input neurons, each of which has a preferred direction $\alpha \in \{0, \pi/4, \pi/2, 3\pi/4, \pi, 5\pi/4, 3\pi/2, 7\pi/4\}$ with each of the 8 cardinal directions represented twice over. We identify these with polarization sensitive TL neurons in the insect central complex (Stone et al., 2017). On each time step they receive input corresponding to the cosine of the difference between their preferred heading and the agent's current heading $\theta \in [0, 2\pi)$:

$$I_{TL} = \cos(\alpha - \theta)\quad (9)$$

2.2.3. Layer 2

The second layer consists of 16 neurons that receive inhibitory input proportional to the output of the first directional input layer. This simple inversion of the response across the array is not actually crucial but is included to model the properties observed in CL1 neurons connecting the polarization input to the protocerebral bridge (Stone et al., 2017).

$$I_{CL1} = -r_{TL} \quad (10)$$

2.2.4. Layer 3 - Compass

The third layer consists of 8 neurons that get input from each pair of CL neurons that have the same directional preference. These neurons are identified with the TB1 neurons in the protocerebral bridge of the CX, which also make mutually inhibitory connections with each other in a specific pattern that resembles a ring-attractor circuit (Stone et al., 2017). Thus, their input is given by:

$$I_{TB1} = W_{CL1,TB1}r_{CL1} + W_{TB1,TB1}r_{TB1} \quad (11)$$

where $W_{CL1,TB1}$ is a $[0, 1]$ matrix mapping pairs of CL neurons to single TB1 neurons, and $W_{TB1,TB1}$ is a matrix of inhibitory weights between TB1 neurons where:

$$W_{TB1_i,TB1_j} = \frac{d(\cos(\alpha_i - \alpha_j) - 1)}{2} \quad (12)$$

where α_i and α_j are the preferred directions of their respective TB1 inputs, and $d = 0.33$ is a scaling factor for the relative effect of this inhibition compared to the direct CL1 excitation.

2.2.5. Layer 4 - Speed Accumulation

The fourth layer consists of 16 neurons, which we associate with the CPU4 cells that occur in each column of the CX central body upper. These receive input from both the protocerebral bridge (TB1) and the noduli (TN2). The input for these neurons is an accumulation of heading of the agent, obtained by inhibitory compass modulation of the speed signal from the speed-sensitive neurons:

$$I_{CPU4_i} = I_{CPU4_{i-1}} + acc \times (r_{TN2_i} - r_{TB1_i} - decay) \quad (13)$$

where r_{TN2} is the speed-sensitive response, r_{TB1} the compass-sensitive response; and $acc = 0.0025$ and $decay = 0.1$ determine the relative rates of memory accumulation and memory loss. The charge of all integrator cells starts at $I_{CPU4_0} = 0.5$ and, as it accumulates, is clipped on each time step to fall between 0 and 1. Note that accumulation occurs on the input, i.e., it is not affected by the non-linearity of the neuron's output function. Also note that the decay shifts the whole activity pattern toward 0, rather than moving the relative amplitude in each accumulator toward the others. As such, this does not act as a leaky integration of the path (as proposed in e.g., Sommer and Wehner, 2004 and as modeled in e.g., Vickerstaff and Di Paolo, 2005), as the relative amplitude will still encode the veridical home vector, unless the leak (or the accumulation) are enough to cause the values to be clipped at 0 (or 1). The 8 TB1 neurons each provide input to two CPU4 neurons which will thus have identical

activity (other than added random noise, see below) as we assume the agent moves in its heading direction thus generating symmetric optic flow. As these neurons integrate the velocity (i.e., speed and direction) of the agent, the activity across this layer at any point in time provides a population encoding of the home vector.

2.2.6. Vector-Memory

This is the only new component in circuit compared to Stone et al. (2017). It is a hypothetical addition and as yet we do not suggest any specific identified neural analog. We store the vector-memory in the synaptic weights of a hypothetical memory neuron that inhibits the output of the CPU4 integrator cells: i.e., the memory neuron has 16 inhibitory output synapses, one per CPU4 output fiber (see **Figures 1B, 2A**).

The weight of these synapses are set according to the corresponding activity of the CPU4 output fiber at the moment of learning, as could be signaled by a reinforcer neuron. More precisely, we store the I_{CPU4} values after passing through a sigmoid function of the same slope and bias parameters as the CPU4 response (see **Supplementary Material**, "Neurons parameters"), but without any added noise. This is to avoid encoding the instantaneous noise level (i.e., the one of the last time step only), and can be interpreted as the learning taking place over a short time interval to more precisely estimate the current CPU4 activity. The noise is then added dynamically (at each time step) during recall, like in the rest of the system. The obtained values are negated in sign (since the synapses are inhibitory). In other words, the agent's current home vector gets stored in the 16 synaptic weights of the memory neuron when the reinforcer neuron is triggered (**Figure 1D**). The learning of the vector-memories is set at particular time or locations: in this paper, these are associated with the discovery of food. As described below, this will allow the agent to return to the position at which the vector was stored. For some experiments we allow the agent to store more than one such vector-memory, into separate memory neurons, corresponding to different food locations.

Thus, the vector-memory synapses can be represented as a 16-values vector W_{VM} :

$$W_{VM} = - \begin{cases} r_{CPU4_{noiseless}}, & \text{if signaled to store} \\ baseline, & \text{otherwise} \end{cases} \quad (14)$$

with *baseline* being a vector of 16 zero-state values (= 0.5, since firing rate is encoded between 0 and 1).

2.2.7. Vector-Memory Recalibration

We also introduce a potential re-calibration of the vector-memories, based on the state of Layer 4 when the agent reaches the nest. In the absence of error (either noise or induced through an experimental manipulation) this state should be zero, so any remaining activation in the Layer 4 thus encodes a possible "error vector" accumulated across the whole path (inbound and/or outbound).

This "error vector" can be used to modulate the vector-memory synapses. For this, another hypothetical process very similar to the learning described above, is used: a "recalibrator"

neuron, triggered when the agent arrives at the nest, modulates the vector-memory synapses that were last active, similarly to the reinforcer neuron used for learning, only differing in the sign of the modulation. That way, the potential “error vector” remaining in the CPU4 population causes the re-calibration of the last active vector-memory (**Figure 4A**).

Thus, the vector-memory W_{VM} update:

$$W_{VM_{rec}} = W_{VM} + r_{rec}(b - r_{CPU4N}) \quad (15)$$

where baseline $b = 0.5$, r_{CPU4N} is the output of the integrator when the Nest is reached, r_{rec} is the activation of the “recalibrator” neuron, or in other words the efficiency of this re-calibration. For instance, with an efficiency $r_{rec} = 1$, the updated vector-memory will be fully corrected for the error. For $r_{rec} = 0.5$ the result will be an average between the previously stored vector-memory and a fully error-corrected one.

2.2.8. Layer 5 - Steering Output

This layer contains 16 neurons which receive input from the compass (layer 3), and the home vector (layer 4) modulated by the vector-memory neuron. These inputs can be switched on or off depending on the agent’s state, e.g., whether it is attempting to return home or to return to the location where a vector was stored. The input from the compass layer 3 is inhibitory, following the same pattern as the layer 3 to layer 4 connections. The connections from layer 4 to layer 5 are offset, by one column to the left for one set of 8 neurons $CPU1_L$, and by one column to the right for the other set of 8 neurons $CPU1_R$. The vector-memory synapses modulate the output from layer 4 to layer 5.

We identify the steering neurons with the CPU1 neurons in the central body upper of the CX, which anatomically reveal the offset pattern used in the model. Inside layer 5 are also pontine neurons that receive the same pattern of input from layer 4, and provide inhibitory output that balances and filters the activity across both hemispheres (see Stone et al., 2017 for more detail). For convenience we neglect the pontine neurons in the equation below because they do not affect the circuit when using symmetric speed input:

$$I_{CPU1} = \begin{cases} W_{TB1,CPU1}r_{TB1}, & \text{when exploring} \\ W_{TB1,CPU1}r_{TB1} + W_{CPU4,CPU1}r_{CPU4}, & \text{when homing} \\ W_{TB1,CPU1}r_{TB1} + W_{CPU4,CPU1}r_{CPU4} + W_{VM}r_{VM} & \text{using vector-memory} \end{cases} \quad (16)$$

where $W_{CPU4,CPU1}$ is the connectivity matrix from CPU4 to CPU1 cells, W_{VM} is synapses weight vector of the vector-memory and r_{VM} is the activation of a specific vector-memory neuron (basically $r_{VM} = 1$ when using that vector-memory, $r_{VM} = 0$ otherwise).

The output of CPU1 cells project to the left and right lateral accessory lobes, which are pre-motor centers. We thus use the difference in $CPU1_L$ and $CPU1_R$ sets to provide a steering signal for the agent:

$$\theta_t = \theta_{t-1} + 0.5 \left(\sum_{i=1}^8 r_{CPU1Li} - \sum_{i=1}^8 r_{CPU1Ri} \right) \quad (17)$$

Note first that in the “exploring” state, the left and right activity will be identical and hence will not affect the steering. In the “homing” state, the circuit effectively performs a comparison of the population vectors representing current heading (compass) ($TB1$) and the integrator $CPU4$, but the connectivity pattern between the integrator and the steering cells means that the desired heading signal is offset in both directions by one column. Hence the left and right activity of the steering cells will represent whether the left or right offset provides a better alignment, and the difference between them can be used to steer, as described in Equation (17). As the integrator keeps running, the steering signal will disappear (or be dominated by noise) when the agent nears home, producing a search pattern.

In the “using vector-memory” state, the output of the integrator is balanced by inhibition from a vector-memory stored at a feeder location (see above). If starting from the nest, with the integrator containing a zero home vector, this negative influence means the agent acts as though its own location (for the purpose of steering) is exactly opposite to where the feeder is located, and the steering circuit will drive it “home” from its actual location (the nest) toward the food. Since the path integration continues to run in parallel, accurately reflecting the agent’s actual displacement, when the food location is reached the input from the integrator to the steering layer will cancel out the negative influence from the vector-memory and the agent will start its search pattern, just as it would at the end of a regular “homing” state.

2.3. Experimental Paradigms

2.3.1. Memory-Directed Movement

To observe the efficiency of the memory-directed movements, the task is realized in two parts: First, the agent performed random walks of different lengths, originating from the nest ($x = 0, y = 0$), and stored for each of these the final integrator state as a new vector-memory. Then, after being reset to the nest (coordinates reset to $x = 0, y = 0$; integrator reset to baseline = 0.5), a vector-memory was recalled and allowed to drive the behavior. We used a feeder catchment area of 20-steps

radius: as soon as the agent entered the feeder catchment area, its proximity sensors guided it to the feeder location. We typically ran $N = 1,000$ trials at 20 random-walk lengths, equally spaced between 100 and 10,000 steps.

A basic measure used was the proportion of successful trials. We considered a food-ward route successful if the agent reached the feeder coordinates within a given time limit of 5,000 steps. It is expected that the agent reaches the target in a straighter path and then performs random search around the expected location. We also evaluated the systematic search patterns produced, either by an agent returning home after a random walk, or an agent using a vector-memory from the nest location to return to the food (see “Systematic search” section in **Supplementary Material**). In this

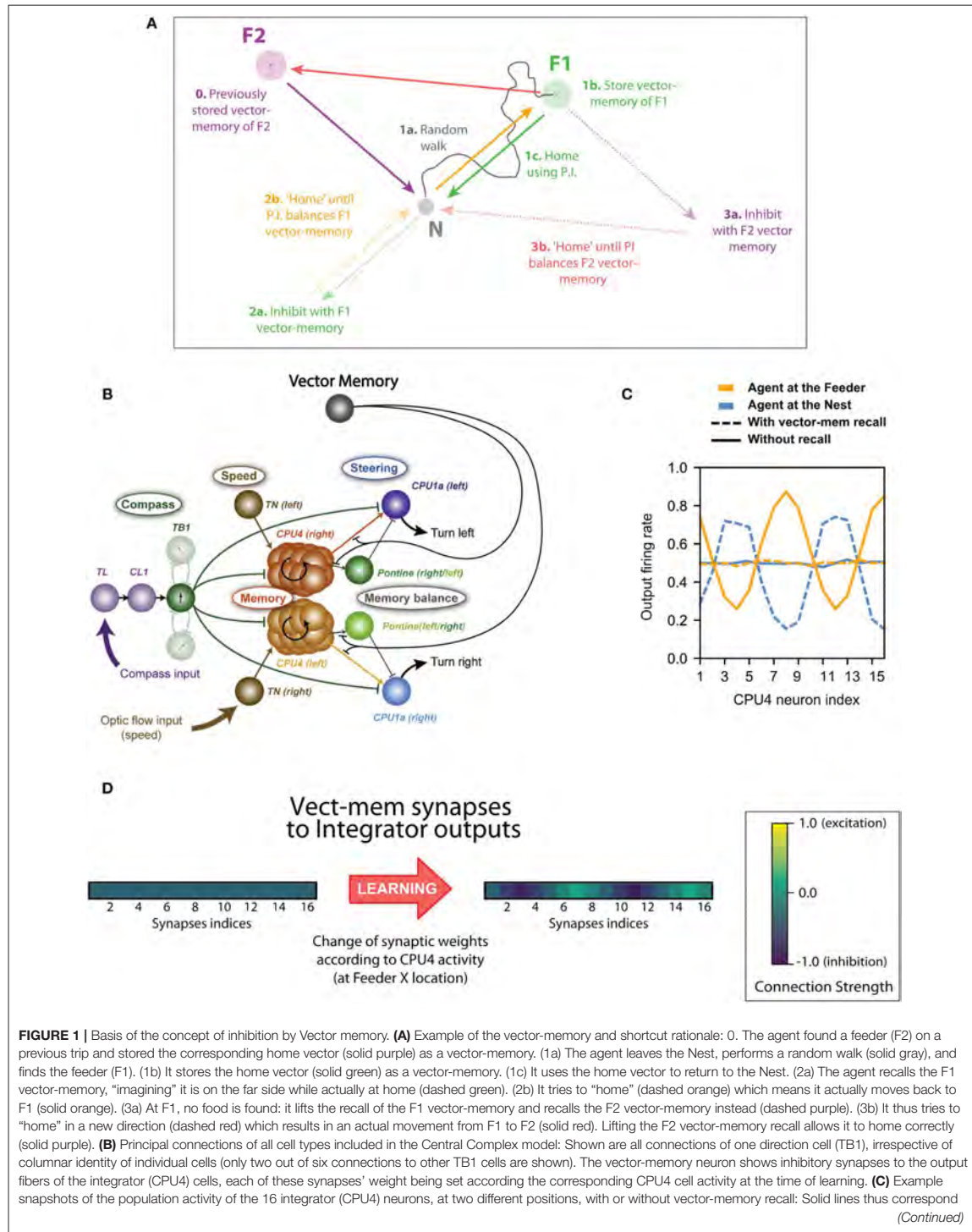


FIGURE 1 | to the output of the integrator, dashed lines to the output of the integrator under the effect of a vector-memory neuron. At the Nest (solid blue), the integrator is in the zero-state (flat line). At the feeder (solid orange), the integrator encodes the position in polar coordinates across the population: sinusoid amplitude is the distance, phase is the angle. Under the inhibition by the vector-memory neuron, when the agent is at the Nest (dashed blue) the apparent coordinates encode for the Nest-to-Feeder vector. At the feeder, still under the effect of the vector-memory neuron (dashed orange), the integrator output and the inhibition cancel out, causing the apparent zero-state. **(D)** Example of the 16 synaptic weights of a vector-memory neuron, before and after learning: Before learning (leftmost vector), the synapses all have a weight of (negative) 0.5. After learning, some synapses get depressed toward 0 (inactive), others get reinforced toward negative 1.0. Each of these weights is changed according to the corresponding integrator (CPU4) cell activity at the time of learning.

case, there was no actual nest or feeder object (or associated catchment area) and instead we allowed the search to continue for 10,000 steps.

2.3.2. Memory Re-calibration

We tested the idea of a vector-memory recalibration in simulated open-jaw experiments, by forcing an incongruity between the outbound and the inbound routes similarly to the experiments of Collett et al. (1999) with ants, and Otto (1959) with bees.

In this task, the agent had first to discover a single feeder location by performing a random walk from its nest in an enclosed area to generate the corresponding vector-memory. Subsequently, we let the agent travel again from the nest to the goal location using its vector-memory. Once this was successfully achieved, we simulated a passive displacement by instantaneously changing its coordinates to a novel release location. We then forced the agent's path back to the nest by using wall obstacles disposed in a gutter-like arrangement (see **Figure 4B**). When the agent reached the nest, its integrator would have recorded the forced displacement but not the passive displacement and will therefore not be at the zero-state. The error vector thus encoded was used to make a correction in the vector-memory as described in section 2.2.

The re-calibrated vector-memory was then used in the test task, for $N = 100$ repetitions. We recorded the paths taken for the averaged re-calibration (eÿciency $r_{rec} = 0.5$), as well as for 10 different values of eÿciency. Note that since we only forced an error during the inbound part, this re-calibration becomes a direct way to change the relative weight of the outbound and inbound routes.

2.3.3. Shortcutting

At any point in a vector-memory enabled walk, the agent is driven by the combined effect of the recalled vector-memory and the current home vector. The agent will try to "home" to the location where these are balanced, even if it is forced to take a detour, or has previously moved by itself to another location (e.g., using the vector-memory of a different feeder). Effectively, this constitutes the subtraction of two vectors: one directed from the agent's current location to the nest, and the second directed from the target feeder location toward the nest, so that its behavior follows the vector between their end-points. In other words, the agent should take a direct shortcut to the second food source.

In our shortcutting experiment, the agent first had to discover independently two feeders, by performing two independent random walks (being reset at the nest in-between these walks), storing the two corresponding vector-memories. Then, it used one of these two memories to go back to the associated feeder as described above in the section 2.3.1 experiment. If the first

goal is reached, the inhibition from this memory is lifted and the second vector-memory is activated. We evaluated the success rate in reaching the second goal, the path straightness during the shortcut, and the angular error when leaving the first feeder.

As in the section 2.3.1 experiment, we generated a large set of vector-memories, by launching sequentially 1,000 outbound random walks, of length varying between 100 and 10,000 steps, binned in 20 equally spaced intervals (i.e., 50 independent random walks per length). We then drew $N = 1,000$ couples of feeders from this bank so that the straight-line distance between the two feeders ranged between 100 and 2,000 steps, binned in 20 equally spaced intervals (i.e., 50 independent repetitions for each of the 20 distances bins), while making sure that the Nest - Feeder 1 distance was as uniformly distributed as possible.

2.3.4. Multi-Location Routes

In our multi-location routes experiments, the agent had as a task to take a multi-feeder route, based on a bank of previously stored vector-memories, before going back to the nest.

The order of feeder visits is based on the fact that the distance between the current location and a given memory location can be obtained from the input to the steering cells after inhibition by a specific vector memory (i.e., the subtraction of the 16 synapse weight values from the 16 CPU4 values). The amplitude of the sinusoidal signal across the 16 values directly correlates with the distance between current and memory location. We used an approximation that would be simple to obtain neurally: the sum of the CPU4 activation values after the subtraction of a given vector memory. Note that alternative approximations for the relative distance could be used, such as the value of the cell that is the most active among the 16 cells.

Given k vector-memories, if each is subtracted in turn from the current integrator state r_{CPU4} , then for each we can define a global activity value $Score_k$ (after clipping the resulting activity between 0 and 1):

$$Score_k = \sum_{i=1}^{16} (r_{CPU4_i} - r_{VM_k_i}) \quad (18)$$

The agent selects the vector-memory generating the smallest $Score_k$ and sets it as the current vector-memory to drive behavior. However, the scoring process is carried out continuously, so at any time it might change to another vector-memory if its score happens to be lower than the current active one. If the agent reaches a feeder at the vector-memory location, it marks that vector as unavailable for recall for the remainder of the trip. Once no vector-memories are available, it will automatically follow its current PI to go home.

We tested this task in three different feeders arrays: a pentagonal array with 5 feeders where nearest neighbor and the optimal routes are equivalent (Lihoreau et al., 2012b), an array with 6 feeders where the nearest neighbor and the optimal route differ (Lihoreau et al., 2012a) in which real bees were found to select the optimal route, and another array with 10 feeders (Ohashi et al., 2006) but in which real bees were not found to select the optimal route.

To see what sequence of feeder visits would emerge for an agent highly familiar with these arrays, we first allowed the agent to discover and store a vector for each feeder in multiple random walks, repeated for an arbitrary high number of discoveries (at least 100 discoveries per feeder). We then averaged the 100 discoveries to obtain a highly accurate vector-memory for each feeder. Then in the tests, an outward trip corresponds to an agent leaving the nest, exploring or following its memories, and going back to the nest either once all feeders have been found or once a time limit is reached. One trial consists of 50 of these outward trips.

To evaluate performance, we looked at the geometry of the routes the agent realized over 500 repeated trials. The success rate was determined by the number of trials where the agent found all feeders and returned to the nest. Considering only the successful trials, we looked at the sequence of feeder visits, on full routes (occurrence of each possible route connecting all the feeders), as well as at individual feeder-to-feeder moves.

To this end, we only logged the actual visit orders and not the vector-memory recall processes. That is to say, if an agent located on feeder A recalled say, vector-memory of feeder B, but actually missed feeder B and found feeder C instead, we counted this as a path from A to C. Revisits to a same feeder were excluded (as per the bee data, e.g., Lihoreau et al., 2012a,b) by making feeders “disappear” from the agent’s detection once they had been visited.

2.3.5. Routes Ontogeny

In order to demonstrate that a route could emerge without necessarily needing the accurate memories used in the previous section, we performed the following experiment on the pentagonal array (Lihoreau et al., 2012b) with a naive agent (without prior knowledge of feeders locations), that gradually learned new food locations through random discovery, while also visiting any locations already learnt:

We here used feeders containing a food amount, and an agent that was assumed to have a crop equal to the sum of all feeders’ food (i.e., the agent could only be fully fed after having visited all the feeders). The agent leaves the nest in a naive state, as it does not possess any vector-memory of the feeders in the test environment. The rule is to use vector-memories if any are available, by recalling them using the previously described process, and if no vector-memory is available, perform a random walk until a feeder is found. We also fix a time limit of 10,000 steps, to prevent any saturation that may occur with longer random walks. When a feeder containing food is discovered through random walk, a new vector-memory is created; if a vector-memory is currently active when a feeder is found, this memory is updated (replaced) by the current integrator state. In both cases this updated/newly created vector-memory is not

made available to recall until after returning to the nest. As with the traplining experiment, the agent returns to the nest only once all feeders have been visited or when the time limit has been reached.

We observed the change in the duration of the outward trips, the change in total distance walked, and the evolution of the visit sequences. Additionally, we looked at the amount of outward trips needed to visit all the feeders, and to visit all the feeders using the optimal route. Note that once all feeders have been visited, the subsequent trips will be equivalent to those in the section 2.3.4, although memories should gradually become more accurate.

3. RESULTS

3.1. Memory-Directed Movement

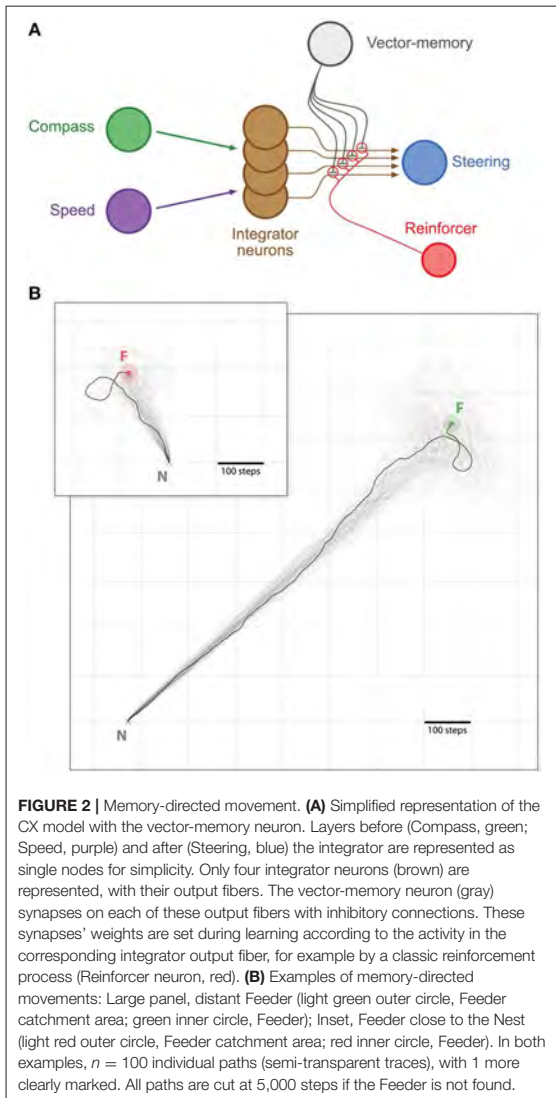
We looked here whether the agent could return from the nest to a location it had reached at the end of a random walk. The agent stored a vector memory at this location, which can be dubbed “feeder location.” We tested 20 random walk distances spanning between 100 and 10,000 steps, with 50 trials per walking distance. To make sure the neurons are not saturating (see **Supplementary Material** section “Saturation” and **Figure S3**), we only used the random walks that ended in a radius of 700 steps from the nest for analysis.

We investigated first the homing performance, by looking whether the agent could home (i.e., reach the nest) from the feeder location. Given an upper limit of 5,000 steps, the success for the homing task was of 100% (0 out 827 trials failed). We then investigated the ability of the agent to return to the feeder location from the nest, using its vector memory. Given an upper limit of 5,000 steps, the rate of success in returning to the feeder location was 93.71% (52 out of 827 trials failed). The paths were rather straight (**Figures 2, 3**), with a straightness index (i.e., beeline/walking distance) of 0.90 for homing and 0.85 for returning to the feeder (which is significantly different for $n = 790$: paired t -test $t = 5.322$, $p < 0.001$). For an analysis of the precision and accuracy of our model in finding the goal, see **Supplementary Material**: Path analysis.

3.2. Memory Re-calibration

We aimed here at capturing the ability of insects to recalibrate the outbound vector-memory based on their last inbound run, which we tested by displacing an insect and forcing a homing route that produces a large outbound-inbound discrepancy, as experimentally achieved in ants (Collett et al., 1999). Over 100 subsequent outward trips, the re-calibrated outward paths resemble closely those of real ants. That is, the agent aims at a location that lies in between the two experimental ones: roughly averaging the distance and direction of the previous outbound and inbound paths (**Figure 4C**).

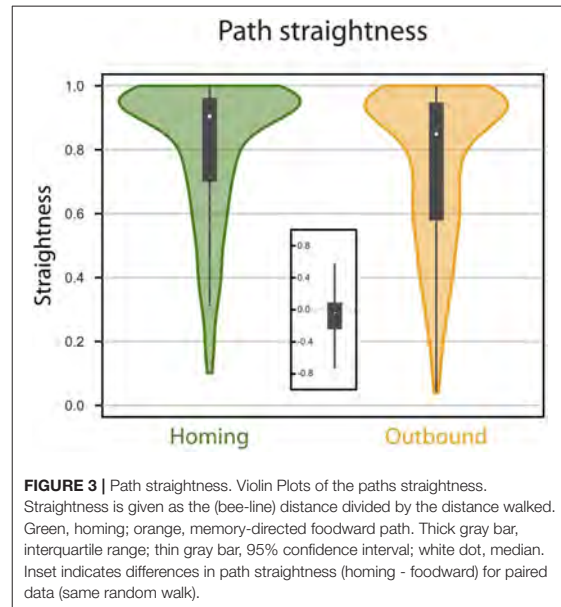
Other studies showed that ants may weight the previous outbound trip more than the inbound trip (Wehner et al., 2002), or even do not recalibrate at all (Wehner and Flatt, 1972). Since the error we introduce is only during the inbound trip, we were able to reproduce these differential weightings of the outbound and inbound trips by varying how much the synaptic weights of



the vector-memory neuron are modulated by the PI state during re-calibration: from paths aiming at the feeder for weak synaptic change to path aiming at the release location for strong synaptic change overriding the previous memory (**Figure 4D**).

3.3. Shortcutting

We tested whether vector-memories could be used to realize novel shortcuts between two known locations. Here the agent has stored two goals as vector-memories, discovered independently. To test for shortcutting, the agent at the nest recalled the memory of a first feeder and, once arrived at this goal, recalled the memory of the second feeder. We observed whether the



agent was able to strike a direct path between the two feeders (**Figure 5**). Here again, to prevent saturation of the neurons (see **Supplementary Material** section “Saturation” and **Figure S3**) we only considered trials where both feeders were within the radius of 700 steps of the nest. Also, we considered only the agents that successfully reached the first feeder (193 out of 212 individuals).

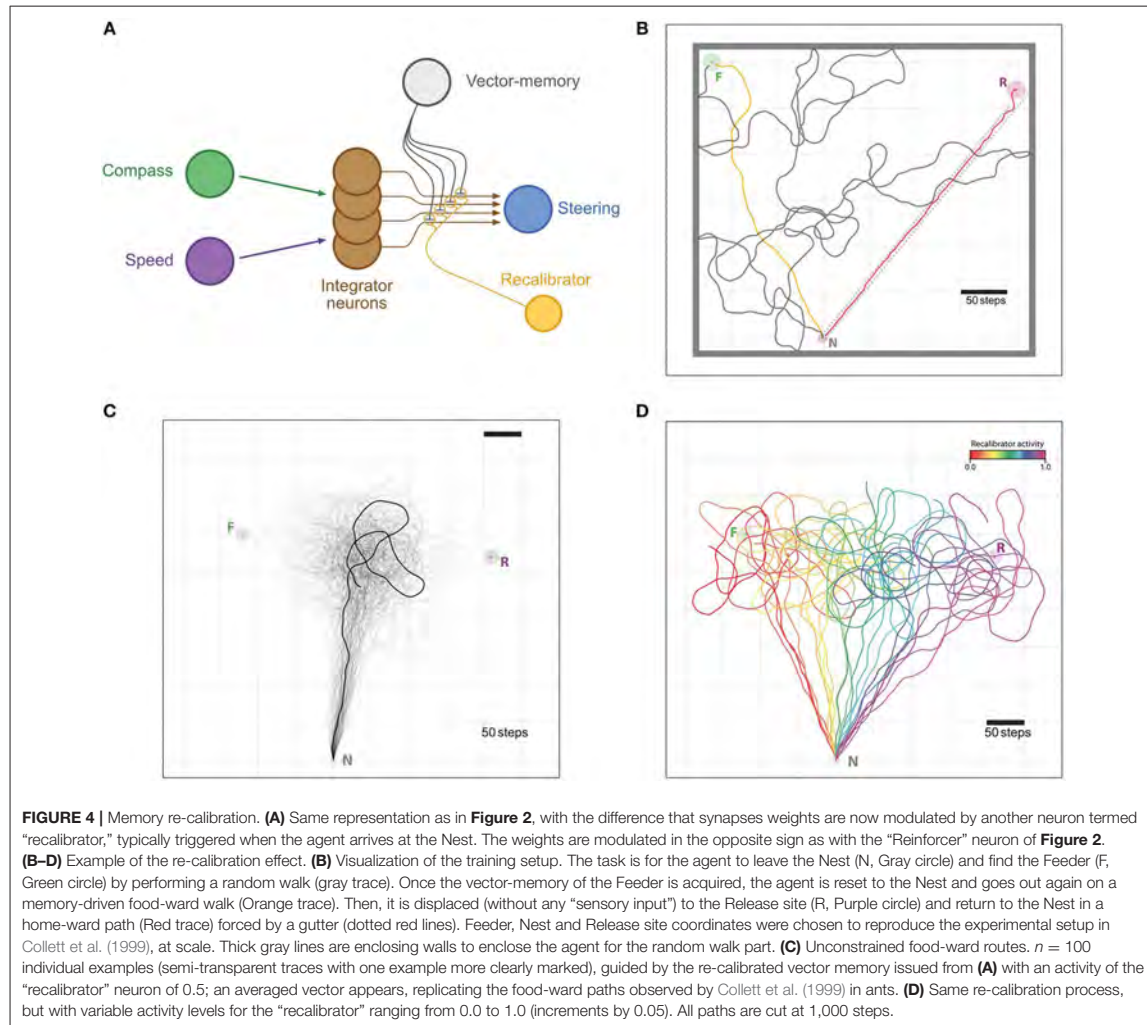
Given an upper limit of 5,000 steps, the rate of success in reaching the second feeder from the first feeder was around 89.6% (20 out of 193 individuals failed to reach Feeder 2 from Feeder 1). We carried an analysis of the directional and positional error of the shortcuts displayed by systematically varying the spatial relationship between the nest and the feeders (see “Shortcutting: Error analysis,” in **Supplementary Material**).

3.4. Multi-Location Routes

We tested whether a route could emerge assuming the agent had memorized multiple feeder locations. In this section, the agent already possesses a vector-memory for each feeder location, and the memories do not change over trials. We use a simple heuristic to decide which vector-memory to recall: the agent recalls the memory that yields the weakest overall output activation after subtraction to the current PI state. We tested three different feeder arrays from the bee literature. For each array, we launched 500 independent trials and observed the sequences of feeders visited within a time limit of $T = 10,000$ steps ($+T_h = 2,500$ steps for homing).

3.4.1. Positive Array (5 Feeders)

We found that 94.20% ($r = 471$) of all trials were successful in the sense that all 5 feeders had been visited and the agent went back to the nest before the time limit (**Figure 6B**). There are $!5 = 120$

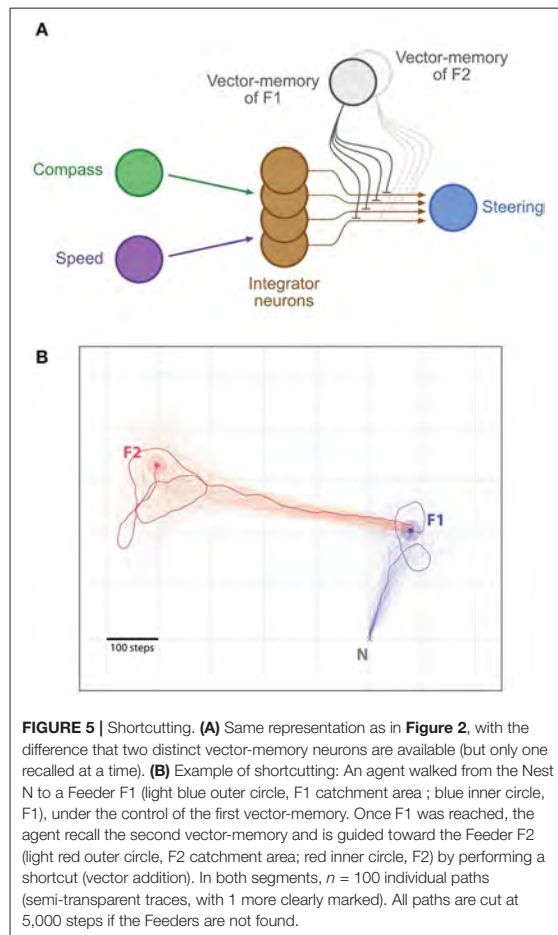


possible routes to visit the 5 feeders in this array. We found that, respectively, 77.71% ($r = 366$) and 15.07% ($r = 71$) of the trials used the two optimal routes (anti-clockwise and clockwise ; 5, 4, 3, 2, 1 and 1, 2, 3, 4, 5, respectively) ; both cases totalling 92.78% ($r = 437$) of trials. The sub-optimal nearest-neighbor routes (1, 5, 4, 3, 2 and 5, 1, 2, 3, 4) were used only in 1.49% ($r = 7$) and 0.64% ($r = 3$), respectively. Two other routes were used in less than 2% of trials, and 6 other routes were used in less than 1% of trials. The other 108 possible routes to join the 5 feeders were never used (see **Supplementary Table 2** for details).

The overall distribution of direct segments effected between pairs of feeders resembles closely that observed in real bees tested in a similar feeder configuration (**Figure 6B**, **Supplementary Table 1**).

3.4.2. Negative Array (6 Feeders)

In this second array, 94.00% ($r = 470$) of all trials were successful. There are $!6 = 720$ possible routes to visit the 6 feeders of this array (**Figure 6C**). Here, only 2.77% ($r = 13$) of the trials used the optimal route (1, 2, 3, 4, 5, 6). However, we found that 47.23% ($r = 222$) of the trials used the second to optimal route (1, 2, 4, 3, 5, 6). This route can be described as “suboptimal” in the sense where it is not the shortest, but it is still better than the nearest-neighbor route (1, 2, 4, 5, 6, 3), which has been used in 41.28% ($r = 194$) of the trials. 2 other routes (2, 1, 4, 5, 6, 3 and 2, 1, 4, 3, 5, 6) were used in, respectively, 3.62% ($r = 17$) and 3.40% ($r = 16$) of trials, and 4 other routes were used in less than 1% of trials. The other 711 possible routes to visit all 6 feeders were never used (see **Supplementary Table 1** for details).



The overall distribution of direct segments effected between pairs of feeders differs from that observed in bees in this similar feeder configuration. This difference arose mostly because the agents did not perform a direct segment between flowers 2 and 3 as often as the bees did (**Figure 6C**), which we discuss later.

3.4.3. Negative Array (10 Feeders)

In this third array, 95.40% ($r = 477$) of all trials were successful. There are $!10 = 3,628,800$ possible routes to visit the 10 feeders of this array (**Figure 6D**). The agent explored a much larger number of different routes (371) than in the previous arrays (12 and 9). No preferred route emerged here, the most used route was displayed in only 2.31% of trials. The four most used routes are not optimal in length nor do they correspond to the nearest-neighbor ones (see **Supplementary Table 3** for details), even though they are closer to the latter. The three next preferred route correspond to optimal routes (clockwise and anti-clockwise rotations, either passing through feeder 1 first, or last), and these

were used in a total of only 1.05% ($r = 5$) of trials. 364 other routes have been used in less than 1% of trials each. The other 3,628,429 possible routes have never been used.

This third array appears to be strongly dependent on stochasticity. This is probably due to a combination of two factors: the short distance between feeders yielding stronger directional inaccuracies (**Figure 6C**, and **Supplementary Table 3**); and the similar distance between different feeders options increases the stochasticity of the recall.

3.5. Routes Ontogeny

We used the positive pentagonal array to test whether such efficient multi-location routes could emerge using a naive agent that needs first to discover the different feeders through random walks (**Figure 7A**). Each time the agent discover a feeder, it stores a new vector-memory that will be available for the next trips. The agent was recorded over 50 successive trips. In each trip, the agent would “home” either after a limit of 10,000 steps or if it has visited all the flower locations (i.e., assuming is crop capacity is filled). Over 20 repetitions of such 50 trips’ ontogeny, the variation and dynamics resembled that of bees in a similar task. The median amount of number trips needed to find all feeders was 12 ($min = 3$, $max = 20$), and the median number of trips needed to realize an optimal route was 13 ($min = 5$, $max = 21$). Interestingly, the optimal route did not necessarily emerge as soon as the 5 feeders were discovered, but was achieved within 0 to 2 trips after. This is because some memories can be at first very noisy due to the long random walks that led to their discovery. Across trials, the memories becomes more precise as the agent reaches the feeders more straightforwardly, and the optimal route eventually emerges (**Figure 7A**).

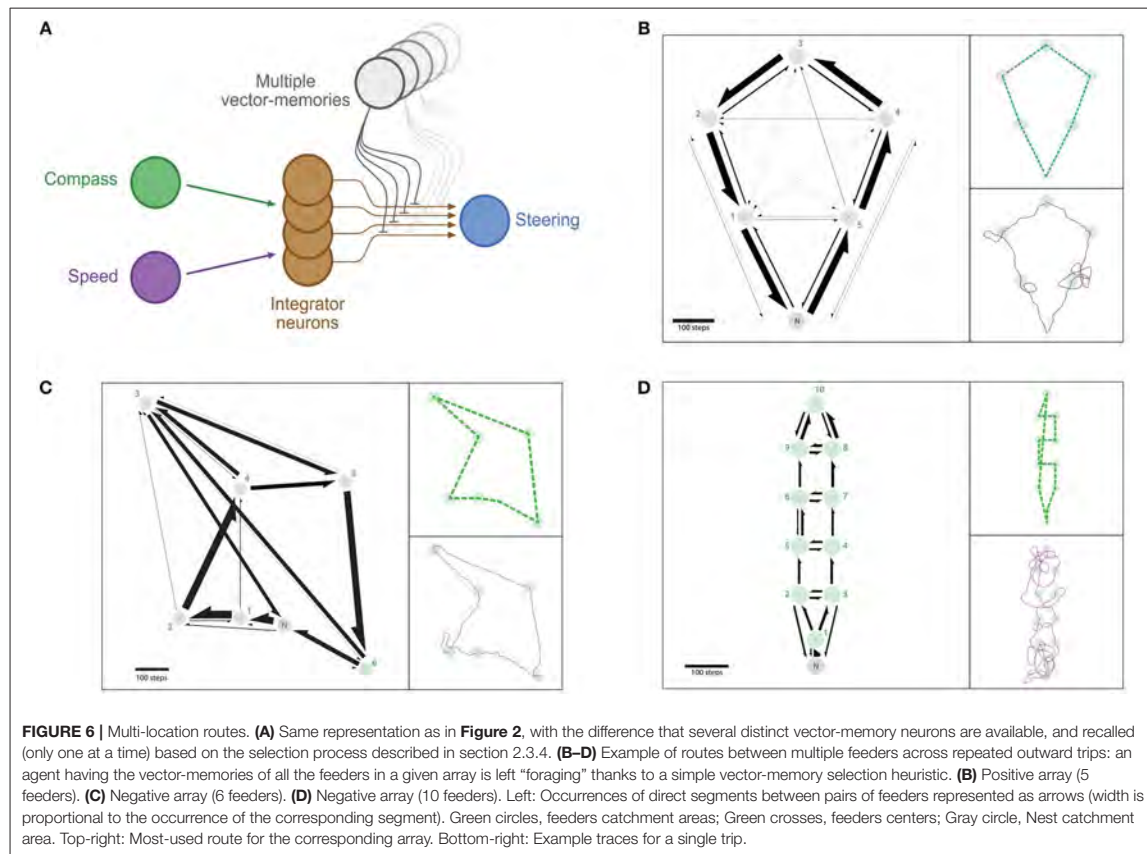
The overall travel distance decreases steadily until reaching a plateau between 20 and 25 trips, close to the shortest straight-line distance. Mean traveling speed increases in a similar dynamic, as fewer turns and straighter segments implies faster movements (**Figure 7B**).

4. DISCUSSION

Insects such as ants and bees are known to use Path Integration (PI) to return in a straight line to their nest (Müller and Wehner, 1988; Collett and Collett, 2000b; Wehner and Srinivasan, 2003), but also store vector-memories to return to a previously experienced location where they have found food (Wehner et al., 1983; Collett et al., 1999; Wolf and Wehner, 2000). These vector-memories can potentially support additional behaviors such as direct shortcuts between food locations, as shown in previous theoretical models (Cruse and Wehner, 2011). Here we demonstrate that a variety of vector-based navigation behaviors can be obtained from simple extensions to a PI model which follows the anatomical connectivity of the central complex (CX) (Stone et al., 2017).

4.1. Vector-Memories and Novel Shortcuts

The key to the functioning of the model is that, during homing, the steering layer of the CX network continuously compares the distributed encoding of the current heading to a left or right



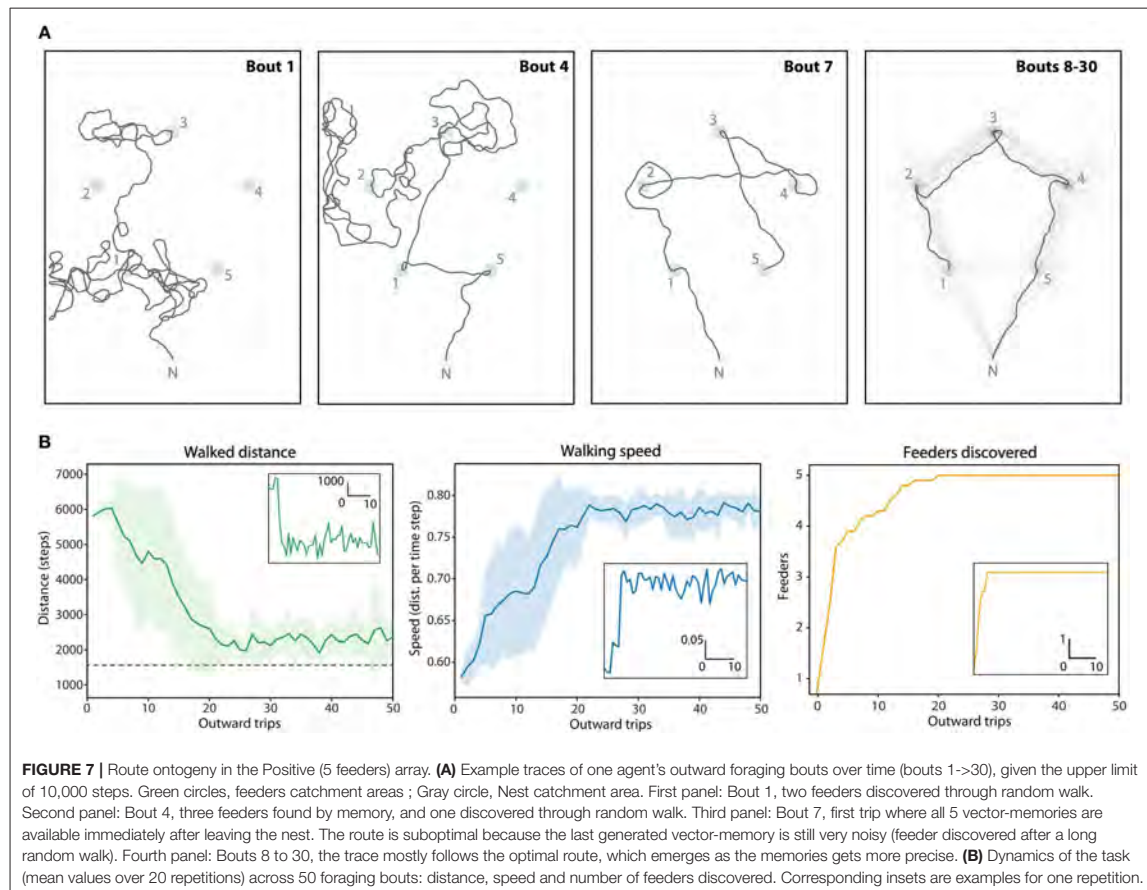
rotation of the distributed encoding of the PI state (the desired heading). This produces an appropriate left or right turn signal to reduce the difference, resulting in a relatively straight path home, at which point the PI state is balanced. In the extended model presented here, the effect of the PI state on steering can be modulated by inhibition from a vector-memory (**Figure 1B**). The balance point will now be the location where the vector-memory was stored (**Figure 1C**), so the same steering circuit produces a direct path to food (**Figure 2**), as observed in insects (Wehner et al., 1983; Schmid-Hempel and Schmid-Hempel, 1984; Collett et al., 1999; Wolf and Wehner, 2000). Removing the inhibitory effects of memory, once the target location is reached, allows steering by the PI state back home again. Alternatively, switching to inhibition by a different vector-memory produces a direct shortcut from the current location to the next goal (**Figure 5**), as observed in bees (Menzel et al., 2005). As for homing, this steering is robust to any imposed deviation from the intended route (Wehner and Srinivasan, 2003). The way vector-memories are compared to the PI state, and can be selected sequentially to produce shortcuts, is functionally equivalent to former models based on Cartesian vectors (Cruse and Wehner, 2011; Hoinville et al., 2012; Hoinville and Wehner, 2018) but in the present

paper it is done with a neurally more plausible ring-neuron representation of vectors.

4.2. Dealing With Inaccuracies

Any PI mechanism necessarily accumulates errors (Cheng et al., 1999; Wehner and Srinivasan, 2003), raising the issue of how insects might deal with such errors. If they do not find the goal, whether home or a food source, insects display a systematic search for it (Fourcassié and Traniello, 1994; Merkle and Wehner, 2009; Schultheiss and Cheng, 2012; Wolf et al., 2012). Similarly, the proposed CX model spontaneously results in a search around the expected goal location (**Figure 2**), as in the original model for homing (Stone et al., 2017) and as well as in another model (Hoinville and Wehner, 2018), suggesting that systematic search may not require an additional “search module,” as often assumed (Wehner, 2009; Cruse and Wehner, 2011; Wystrach et al., 2013).

The question of PI errors also raises the question of whether and how insects might recalibrate their memories. We introduced two mechanisms by which a vector memory might become more accurate. The first follows from the analysis above—there will be less error in the PI state if the animal reaches a food location on a more direct path from the nest, so



increasing precision can be obtained by updating the “active” vector-memory, when the goal is reached, with the current PI value, as we observe in route ontogeny (Figure 7A).

There is some evidence in insects of a second mechanism. Manipulating the return path from a food source to the nest can affect the vector-memory (Otto, 1959; Collett et al., 1999; Bolek et al., 2012). We showed how this could be effected in our CX model by allowing the vector memory stored at a goal location (the set of weights) to be adjusted, when the agent has reached home, proportionally to the remaining PI signal, which denotes accumulated errors. This recalibration simply requires the same assumed synaptic connectivity than for learning a vector-memory at the first place (Figure 4A). It only implies a second instant in which synaptic weights are altered, rather than an independent PI system for outbound vs. inbound routes. Note that this adjustment could be done simultaneously for all memories either formed or activated on the most recent journey.

In insects, the influence of the homeward path on the next outbound paths varies across experiments (Wehner et al., 2002; Menzel and Greggers, 2015), or sometimes seems

non-existent (Wehner and Flatt, 1972). In our model, such variation can be achieved by changing the strength of the synaptic modulation applied during recalibration (Figure 4). This effectively results in using different proportions of the PI error when making this adjustment (Figure 4D). It remains unclear whether these differences result from differences in species, motivational state, environmental circumstances or individual experience.

Of the “memory neuron” accordingly to the remaining activity of the neurons onto which they synapse. That is, similarly to the way we suggest vector-memory are learnt in the first place, excepted that the synaptic modulation is in the opposite direction, and should happen once the agent has reached home.

4.3. Multi-Feeder Routes

We further extended the shortcut process to explain the development and maintenance of efficient routes between multiple feeders as exhibited by bees (Ohashi et al., 2006; Lihoreau et al., 2012b; Buatois and Lihoreau, 2016). This required two assumptions: 1-the agent needs to select one vector-memory

at a time, and 2-a memory becomes unavailable once that location has been visited. We implemented a simple continuous memory selection mechanism, as has been previously proposed (Hoinville et al., 2012). To do so, we used the fact that, in the CX circuit, the inhibition of a target vector-memory onto the PI results in activation levels which amplitude is proportional to the distance to be traveled (Figure 1C). At each time step, the current vector-memory recalled can thus be the one that results in the smallest amplitude. Several proxies could be used to approximate this amplitude, but how this is implemented neurally remain to be seen. This produced multi-location routes in our agent that are surprisingly similar to that of bees (Figure 6), including the discovery of optimal (shortest possible) routes for some feeder arrays (Lihoreau et al., 2012b), and less optimal routes for other layouts (Ohashi et al., 2006; Woodgate et al., 2017). Alternative hypotheses for memory-selection could exist, but a continuously running winner-take-all mechanism seems parsimonious and readily testable: for example, by enforcing a detour toward a feeder B to a bee on its way to a feeder A and looking for an eventual motivational switch from A to B.

Different ways of storing and selecting vector memories might result in slightly different multi-feeder route outcomes, but the key point is that bees would not need to store, nor compare any additional information (such as path length) about previous journeys to be able to improve their performance over time. Importantly, in this model such multi-feeder routes do emerge, no matter the memory selection mechanism, and without the need to make a comparison of the total traveled distances across successive paths, which was assumed in previous theoretical models (Lihoreau et al., 2012b; Reynolds et al., 2013).

Note that in one of the arrays, the preferred route adopted by our model was not the preferred route of the real bees, but their second preferred one (Figure 6C). However, insects do not rely only on vector based strategies, and additional mechanisms, such as the use of terrestrial cues, are likely to modulate the way they follow routes. Spontaneous bias may also influence the shape of a route. For instance, bumblebees have a natural tendency to depart from a flower in the same direction as they arrived (Pyke and Cartar, 1992), which we did not implement here.

Finally, our model could also produce a realistic ontogeny of such multi-feeder routes (note however that we tried here only the regular pentagonal array), given the simple assumption that an agent with no vector-memory available to recall triggers a random walk (Figure 7A). In this case vector-memories are gradually added as the agent discovers new flowers. As a consequence, paths become straighter and the revisits order becomes more efficient across successive trips (Figure 7A). Interestingly, the ontogeny dynamics of our agents in the pentagon array (Figure 7B) resembles that of real bees (see [Supplementary Material](#) for more details).

4.4. Insights Into Behavior?

Our study thus shows that for direct return to a goal, search around the goal location, shortcuts between goals and efficient route discovery between multiple goals, vector manipulation is a highly parsimonious explanation for observed insect behavior because it appears strongly consistent with

the known architecture, and likely computational function, of the CX.

Can our proposed CX implementation however provide predictions about systematic errors in insects, over and above that which has already been provided by canonical PI models (Cheung and Vickerstaff, 2010; Vickerstaff and Cheung, 2010; Cheung, 2014; Hoinville and Wehner, 2018)? We note that the effective PI calculation carried out by our CX circuit model is equivalent to an allocentric Cartesian encoding, and as such, theoretical results concerning the effects of sensory or internal noise on accuracy and precision in return to home or a vector goal derived from mathematical models of this form (Cheung and Vickerstaff, 2010; Cheung, 2014; Hoinville and Wehner, 2018) should apply. This is broadly true for our simulation (see detailed analysis in [Supplementary Material](#)). For example, we find that directional precision (perhaps counterintuitively) increases with nest-feeder distance, for both inbound and outbound paths, and does not depend on the length of the random walk made before discovery of the feeder, which is consistent with both canonical PI models (Hoinville and Wehner, 2018) and results in ants (Wystrach et al., 2015).

However, we note that observed error effects may be dependent on particular, and somewhat arbitrary, choices in our neural and/or behavioral modeling. For instance, we believe the non-linear activation function of neurons used in the model may explain some of the errors observed, such as an underestimation of distance (see [Supplementary Material](#)). It is also possible that some of our results are a consequence of (equally arbitrary) parameters in our random walk model (Cheung, 2014). Examination of the consequences of varying these choices would be interesting but is beyond the scope of this paper, which aims to provide a proof-of-principle, rather than provide strong quantitative predictions about animal behavior. However, one general outcome that should hold is that errors for foodward routes should always be higher on average than for homeward routes, as observed here (Figure 3), because the control depends on both the current noise in PI and the noise in the vector-memory, from the PI state when it was stored. As the focus of this paper was to show an “in principle” mechanism for vector memory in the insect brain, we leave more detailed examination of how parameter choices in the CX model might affect errors to future work.

4.5. Insights Into Neural Circuits

It is of interest to consider whether the neurobiological assumptions made in our model could be verified:

- We modeled vector-memory as simple storage of a copy of the 16 discrete values in the CPU4 layer that represent the home vector at that point in time. We suggest that a vector-memory could be encoded by a single “vector-memory neuron” that sends inhibitory connections to the output of all the integrator neurons (Figure 2A). We therefore suggest the existence of such inhibitory neuron projecting to all wedges of the CPU4 outputs or analogous CX layers that would also encode current PI state. Note that similar global inhibitor neurons have been evidenced in *Drosophila* (Kim et al., 2017).

- Learning a vector-memory would therefore consist in setting the weights of such inhibitory connections. Each output synapse of the vector-memory neuron should be weighted according to the neural activity of CPU4 neuron onto which it synapses, when at the feeder. Such synaptic modulation could be achieved by a reinforcer neuron triggered by the food intake at the feeder (**Figure 4A**). Likely candidates are dopaminergic (Kong et al., 2010) or octopaminergic (Wolff and Rubin, 2018) neurons that are known to project into the central complex.
- Re-calibration would consist in modulating the output synapses of a learnt vector-memory neuron. As for learning, synaptic weight should be modulated according to the activity of the CPU4, but in the opposite direction and when the agent is at home. Such bi-directional synaptic modulation for learning and recalibration could be achieved either by a same or different reinforcer neuron (Aso and Rubin, 2016).
- The establishment of a new vector-memory, as well as vector re-calibration, implies long term synaptic change between the hypothesized memory neurons and the CPU4 neurons. Thus, inhibiting long term memory formation in these neurons (e.g., Chen et al., 2012) should prevent the establishment (or re-calibration) of these vector-memories.
- Recall of a vector-memory would simply require the activation of this vector-memory inhibitory neuron, and drive the agent from any location to where the memory has been stored.
- Blocking the activity of such inhibitory neuron should prevent the use of a vector-memory, while driving it should lead the insect to go toward the position in space where the memory has been formed.
- The distributed encoding of vectors in our model provides a simple way to estimate the length of the home vector: by taking the difference in amplitude between the highest and lowest neural activities in the CPU4 integrator layer. Doing so on the resulting vector created by the added inhibitory input of a vector-memory would therefore give a rough estimate of the distance to be covered from the current location to that memory location.

We note that none of these predictions would be trivial to test. However, observing or manipulating the activation of such neural populations in the CX can already be achieved in *Drosophila melanogaster* (Seelig and Jayaraman, 2015; Kim et al., 2017), and local path integration has also been observed in this animal (Kim and Dickinson, 2017). We further hope that modern genetic tools will soon make this endeavor possible in insects such as bees or ants.

REFERENCES

- Aso, Y., and Rubin, G. M. (2016). Dopaminergic neurons write and update memories with cell-type-specific rules. *Elife* 5:e16135. doi: 10.7554/eLife.16135
- Bolek, S., Wittlinger, M., and Wolf, H. (2012). Establishing food site vectors in desert ants. *J. Exp. Biol.* 215, 653–656. doi: 10.1242/jeb.062406
- Buatois, A., and Lihoreau, M. (2016). Evidence of trapline foraging in honeybees. *J. Exp. Biol.* 219, 2426–2429. doi: 10.1242/jeb.143214

5. CONCLUSION

The PI model presented in Stone et al. (2017) was mostly based on identified neurons in the CX, whereas the extensions we have proposed here are speculative. Nevertheless, we have provided a proof of concept that direct return to a salient place, search at this locations, vector recalibration, novel shortcuts and even traplining can emerge given minimal additions to the known CX connectivity. A direction for future work would be to consider how such PI navigation system could be integrated with the use of learnt terrestrial cues, which we know affects how bees and ants behave when homing or returning to a known feeding location (Kohler and Wehner, 2005; Wystrach et al., 2011; Mangan and Webb, 2012; Collett et al., 2013), search at the goal (Schultheiss et al., 2013; Wystrach et al., 2013), take shortcuts from novel locations (Menzel et al., 2005; Collett et al., 2007; Wystrach et al., 2012; Narendra et al., 2013; Cheeseman et al., 2014; Cheung et al., 2014), or form traplines between multiple locations (Ohashi et al., 2006; Lihoreau et al., 2012b). The circuitry of the CX is well suited for such an integration of multiple directional cues (Webb and Wystrach, 2016; Collett and Collett, 2018; Hoinville and Wehner, 2018), and as we show here, for a remarkably rich vector-based navigational repertoire.

AUTHOR CONTRIBUTIONS

FL and TS: model implementation; FL, AW, and BW: manuscript writing; FL, ML, AW, and BW: manuscript reviewing; FL, TS, AW, and BW: conceptual ideas.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsyg.2019.00690/full#supplementary-material>

- Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D., Gallistel, C. R., et al. (2014). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *Proc. Natl. Acad. Sci. U.S.A.* 111, 8949–8954. doi: 10.1073/pnas.1408039111
- Chen, C.-C., Wu, J.-K., Lin, H.-W., Pai, T.-P., Fu, T.-F., Wu, C.-L., et al. (2012). Visualizing long-term memory formation in two neurons of the drosophila brain. *Science* 335, 678–685. doi: 10.1126/science.1212735

- Cheng, K., Srinivasan, M. V., and Zhang, S. W. (1999). Error is proportional to distance measured by honeybees: Weber's law in the odometer. *Anim. Cogn.* 2, 11–16. doi: 10.1007/s100710050020
- Cheung, A. (2014). Animal path integration: a model of positional uncertainty along tortuous paths. *J. Theor. Biol.* 341, 17–33. doi: 10.1016/j.jtbi.2013.09.031
- Cheung, A., Collett, M., Collett, T. S., Dewar, A., Dyer, F., Graham, P., et al. (2014). Still no convincing evidence for cognitive map use by honeybees. *Proc. Natl. Acad. Sci. U.S.A.* 111, E4396–E4397. doi: 10.1073/pnas.1413581111
- Cheung, A., and Vickerstaff, R. (2010). Finding the way with a noisy brain. *PLoS Comput. Biol.* 6:e1000992. doi: 10.1371/journal.pcbi.1000992
- Collett, M., Chittka, L., and Collett, T. S. (2013). Spatial memory in insect navigation. *Curr. Biol.* 23, R789–R800. doi: 10.1016/j.cub.2013.07.020
- Collett, M., and Collett, T. S. (2000a). How do insects use path integration for their navigation? *Biol. Cybern.* 83, 245–259. doi: 10.1007/s004220000168
- Collett, M., and Collett, T. S. (2018). How does the insect central complex use mushroom body output for steering? *Curr. Biol.* 28, R733–R734. doi: 10.1016/j.cub.2018.05.060
- Collett, M., Collett, T. S., and Wehner, R. (1999). Calibration of vector navigation in desert ants. *Curr. Biol.* 9, 1031–S1. doi: 10.1016/S0960-9822(99)80451-5
- Collett, M., Graham, P., and Collett, T. S. (2017). Insect navigation: what backward walking reveals about the control of movement. *Curr. Biol.* 27, R141–R144. doi: 10.1016/j.cub.2016.12.037
- Collett, T., Graham, P., and Harris, R. (2007). Novel landmark-guided routes in ants. *J. Exp. Biol.* 210, 2025–2032. doi: 10.1242/jeb.000315
- Collett, T. S., and Collett, M. (2000b). Path integration in insects. *Curr. Opin. Neurobiol.* 10, 757–762. doi: 10.1016/S0959-4388(00)00150-1
- Cruse, H., and Wehner, R. (2011). No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comput. Biol.* 7:e1002009. doi: 10.1371/journal.pcbi.1002009
- Fourcassié, V., and Traniello, J. F. (1994). Food searching behaviour in the ant *formica schaufussi* (hymenoptera, formicidae): response of naive foragers to protein and carbohydrate food. *Anim. Behav.* 48, 69–79. doi: 10.1006/ange.1994.1212
- Hoinville, T., and Wehner, R. (2018). Optimal multiguideance integration in insect navigation. *Proc. Natl. Acad. Sci. U.S.A.* 115, 2824–2829. doi: 10.1073/pnas.1721668115
- Hoinville, T., Wehner, R., and Cruse, H. (2012). "Learning and retrieval of memory elements in a navigation task," in *Conference on Biomimetic and Biohybrid Systems* (Barcelona: Springer), 120–131.
- Kim, I. S., and Dickinson, M. H. (2017). Idiopathic path integration in the fruit fly *drosophila melanogaster*. *Curr. Biol.* 27, 2227–2238. doi: 10.1016/j.cub.2017.06.026
- Kim, S. S., Rouault, H., Druckmann, S., and Jayaraman, V. (2017). Ring attractor dynamics in the *drosophila* central brain. *Science* 356, 849–853. doi: 10.1126/science.aal4835
- Kohler, M., and Wehner, R. (2005). Idiosyncratic route-based memories in desert ants, *melophorus bagoti*: how do they interact with path-integration vectors? *Neurobiol. Learn. Mem.* 83, 1–12. doi: 10.1016/j.nlm.2004.05.011
- Kong, E. C., Woo, K., Li, H., Lebestky, T., Mayer, N., Sniffen, M. R., et al. (2010). A pair of dopamine neurons target the d1-like dopamine receptor *dopr* in the central complex to promote ethanol-stimulated locomotion in *drosophila*. *PLoS ONE* 5:e9954. doi: 10.1371/journal.pone.0009954
- Labhart, T., and Meyer, E. P. (2002). Neural mechanisms in insect navigation: polarization compass and odometer. *Curr. Opin. Neurobiol.* 12, 707–714. doi: 10.1016/S0959-4388(02)00384-7
- Lihoreau, M., Chittka, L., Le Comber, S. C., and Raine, N. E. (2012a). Bees do not use nearest-neighbour rules for optimization of multi-location routes. *Biol. Lett.* 8, 13–16. doi: 10.1098/rsbl.2011.0661
- Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J., Lim, K. S., Smith, A. D., et al. (2012b). Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. *PLoS Biol.* 10:e1001392. doi: 10.1371/journal.pbio.1001392
- Mangan, M., and Webb, B. (2012). Spontaneous formation of multiple routes in individual desert ants (*cataglyphis velox*). *Behav. Ecol.* 23, 944–954. doi: 10.1093/beheco/ars051
- Menzel, R., and Greggers, U. (2015). The memory structure of navigation in honeybees. *J. Compar. Physiol. A* 201, 547–561. doi: 10.1007/s00359-015-0987-6
- Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., et al. (2005). Honey bees navigate according to a map-like spatial memory. *Proc. Natl. Acad. Sci. U.S.A.* 102, 3040–3045. doi: 10.1073/pnas.0408550102
- Merkle, T., and Wehner, R. (2009). How flexible is the systematic search behaviour of desert ants? *Anim. Behav.* 77, 1051–1056. doi: 10.1016/j.anbehav.2009.01.006
- Müller, M., and Wehner, R. (1988). Path integration in desert ants, *cataglyphis fortis*. *Proc. Natl. Acad. Sci. U.S.A.* 85, 5287–5290. doi: 10.1073/pnas.85.14.5287
- Narendra, A., Gourmaud, S., and Zeil, J. (2013). Mapping the navigational knowledge of individually foraging ants, *myrmecia croslandi*. *Proc. R. Soc. Lond. B Biol. Sci.* 280:20130683. doi: 10.1098/rspb.2013.0683
- Ohashi, K., Thomson, J. D., and D'souza, D. (2006). Trapline foraging by bumble bees: IV. optimization of route geometry in the absence of competition. *Behav. Ecol.* 18, 1–11. doi: 10.1093/beheco/arl053
- Otto, F. (1959). Die bedeutung des rückfluges für die richtungs-und entfernungsangabe der bienen. *Zeitschrift für Vergleichende Physiologie* 42, 303–333. doi: 10.1007/BF00298124
- Pfeffer, S. E., and Wittlinger, M. (2016). How to find home backwards? navigation during rearward homing of *cataglyphis fortis* desert ants. *J. Exp. Biol.* 219, 2119–2126. doi: 10.1242/jeb.137786
- Pyke, G., and Cartar, R. (1992). The flight directionality of bumblebees: do they remember where they came from? *Oikos* 65, 321–327. doi: 10.2307/3545025
- Reynolds, A. M., Lihoreau, M., and Chittka, L. (2013). A simple iterative model accurately captures complex trapline formation by bumblebees across spatial scales and flower arrangements. *PLoS Comput. Biol.* 9:e1002938. doi: 10.1371/journal.pcbi.1002938
- Riley, J., Reynolds, D., Smith, A., Edwards, A., Osborne, J., Williams, I., et al. (1999). Compensation for wind drift by bumble-bees. *Nature* 400:126. doi: 10.1038/22029
- Schmid-Hempel, P., and Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *cataglyphis bicolor* (hymenoptera, formicidae). *Insect. Sociaux* 31, 345–360. doi: 10.1007/BF02223652
- Schultheiss, P., and Cheng, K. (2012). Finding food: outbound searching behavior in the Australian desert ant *melophorus bagoti*. *Behav. Ecol.* 24, 128–135. doi: 10.1093/beheco/ars143
- Schultheiss, P., Wystrach, A., Legge, E. L., and Cheng, K. (2013). Information content of visual scenes influences systematic search of desert ants. *J. Exp. Biol.* 216, 742–749. doi: 10.1242/jeb.075077
- Schwarz, S., Mangan, M., Zeil, J., Webb, B., and Wystrach, A. (2017). How ants use vision when homing backward. *Curr. Biol.* 27, 401–407. doi: 10.1016/j.cub.2016.12.019
- Seelig, J. D., and Jayaraman, V. (2015). Neural dynamics for landmark orientation and angular path integration. *Nature* 521:186. doi: 10.1038/nature14446
- Sommer, S., and Wehner, R. (2004). The ant's estimation of distance travelled: experiments with desert ants, *cataglyphis fortis*. *J. Compar. Physiol. A* 190, 1–6. doi: 10.1007/s00359-003-0465-4
- Stone, T., Webb, B., Adden, A., Weddig, N. B., Honkanen, A., Templin, R., et al. (2017). An anatomically constrained model for path integration in the bee brain. *Curr. Biol.* 27, 3069–3085. doi: 10.1016/j.cub.2017.08.052
- Stürzl, W., Zeil, J., Boeddeker, N., and Hemmi, J. M. (2016). How wasps acquire and use views for homing. *Curr. Biol.* 26, 470–482. doi: 10.1016/j.cub.2015.12.052
- Vickerstaff, R., and Di Paolo, E. (2005). Evolving neural models of path integration. *J. Exp. Biol.* 208, 3349–3366. doi: 10.1242/jeb.01772
- Vickerstaff, R. J., and Cheung, A. (2010). Which coordinate system for modelling path integration? *J. Theor. Biol.* 263, 242–261. doi: 10.1016/j.jtbi.2009.11.021
- Webb, B., and Wystrach, A. (2016). Neural mechanisms of insect navigation. *Curr. Opin. Insect Sci.* 15, 27–39. doi: 10.1016/j.cois.2016.02.011
- Wehner, R. (2009). The architecture of the desert ant's navigational toolkit (hymenoptera: Formicidae). *Myrmecol News* 12, 85–96.
- Wehner, R., and Flatt, I. (1972). "The visual orientation of desert ants, *cataglyphis bicolor*, by means of terrestrial cues," in *Information Processing in the Visual Systems of Anthropods* (Berlin; Heidelberg; New York, NY: Springer), 295–302.
- Wehner, R., Gallizzi, K., Frei, C., and Vesely, M. (2002). Calibration processes in desert ant navigation: vector courses and systematic search. *J. Compar. Physiol. A* 188, 683–693. doi: 10.1007/s00359-002-0340-8

- Wehner, R., Harkness, R. D., and Schmid-Hempel, P. (1983). *Foraging Strategies in Individually Searching Ants*. Stuttgart: Fischer.
- Wehner, R., and Srinivasan, M. V. (2003). "Path integration in insects," in *The Neurobiology of Spatial Behaviour*, ed K. J. Jeffery (Oxford: Oxford University Press), 9–30. doi: 10.1093/acprof:oso/9780198515241.003.0001
- Wolf, H., and Wehner, R. (2000). Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *cataglyphis fortis*. *J. Exp. Biol.* 203, 857–868.
- Wolf, H., Wittlinger, M., and Bolek, S. (2012). Re-visiting of plentiful food sources and food search strategies in desert ants. *Front. Neurosci.* 6:102. doi: 10.3389/fnins.2012.00102
- Wolff, T., and Rubin, G. M. (2018). Neuroarchitecture of the drosophila central complex: a catalog of nodulus and asymmetrical body neurons and a revision of the protocerebral bridge catalog. *J. Compar. Neurol.* 526, 2585–2611. doi: 10.1002/cne.24512
- Woodgate, J. L., Makinson, J. C., Lim, K. S., Reynolds, A. M., and Chittka, L. (2017). Continuous radar tracking illustrates the development of multi-destination routes of bumblebees. *Sci. Rep.* 7:17323. doi: 10.1038/s41598-017-17553-1
- Wystrach, A., Beugnon, G., and Cheng, K. (2012). Ants might use different view-matching strategies on and off the route. *J. Exp. Biol.* 215, 44–55. doi: 10.1242/jeb.059584
- Wystrach, A., Mangan, M., and Webb, B. (2015). Optimal cue integration in ants. *Proc. R. Soc. B* 282:20151484. doi: 10.1098/rspb.2015.1484
- Wystrach, A., Schwarz, S., Baniël, A., and Cheng, K. (2013). Backtracking behaviour in lost ants: an additional strategy in their navigational toolkit. *Proc. R. Soc. Lond. B Biol. Sci.* 280:20131677. doi: 10.1098/rspb.2013.1677
- Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G., and Cheng, K. (2011). Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *J. Compar. Physiol. A* 197, 167–179. doi: 10.1007/s00359-010-0597-2

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Chapter 2

InsectVisionSimulator: an interface for visual navigation models in Python

Florent Le Moël and Jan Stankiewicz, Antoine Wystrach and Barbara Webb



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Introduction

The ability of insects such as ants, wasps, or bees to navigate skilfully in complex environments using vision is a remarkable example of the powers of their tiny brains. In the last decade, we have greatly improved our understanding of the mechanisms underlying these behaviours. The field of insect navigation has benefited from a combination of behavioural experiments deeply rooted in an ecologically-significant framework, with thorough description of natural behaviours and the surrounding natural environments [39, 52, 137, 332, 342], as well as detailed explorations of the brains circuits underlying navigational skills [172, 300, 232, 117, 115, 92, 237].

Understanding insect navigation behaviour is far from trivial because observed actions are not merely a consequence of brain activity, rather they emerge from closed-loop systems involving complex dynamics between the animals' brain, body and environment. This inter-dependency is crucial but often overlooked [13, 37]. These dynamics are hard to intuit because the interactions usually happen in parallel and are typically non-linear. In addition, the elements of the system (i.e., the brain, body position and perceived environment) are constantly changing, further increasing the challenge. In order to understand an animal's behaviour, its Umwelt, personal experience and the environment in which it has evolved must be considered. Where Umwelt is defined as the way in which its sensory system filters the environment. [81, 297, 332]. Such Umwelts and complex dynamics can be uniquely explored using computational modelling. Studies involving agent-based simulations have transpired to be useful in advancing our understanding of insect navigation [i.e., 50, 10, 54, 110]. In recent years, incorporating anatomically constrained neural circuits into the agent's logic has further improved the utility of this approach by providing a unique understanding of the link between behaviour, neurobiology and ecology [5, 271, 263]. Another recent development is the availability of lidar scans of animal habitats which provides a high-fidelity model to deploy simulations in. However, such a modelling approach can be strongly slowed down by the need to manipulate complex 3D environments and render insect eye views, which involve cumbersome calculations at each step of the agent.

To eschew these problems we provide *InsectVisionSimulator*, a Python package that facilitates rapid simulation of complex 3D worlds for animal behaviour modelling.

One aspect of insect vision that can't be achieved with conventional simulation environments is the role of compound eyes, structures that sample the visual environment through multiple independent light detecting units, called ommatidia, each typically with a narrow field of view. The ability to render the visual information through an insect's compound eye is therefore another element that is included in the current work. Our Python package is modular and can be easily accommodated to the level of complex-

ity required, from studies focusing on neural visual processing, learning and memory, to sensory-motor dynamics, or all of these simultaneously.

Methods

InsectVisionSimulator is a one-stop-shop package for simulating vision-lead animal behaviours. In addition to the tools provided for rendering 3D environments, an *application interface* (API) for moving animals around this world is provided.

The package is subdivided into three modules:

1. the *environment* module, which handles the I/O of mesh data and simple physics computation for movements in the 3D environment
2. the *engine* module, which performs all onscreen and offscreen rendering tasks
3. an *insect_eye* module which aims at simulating the views obtainable from highly customizable faceted eyes. Each of these modules are designed to work together in a complete suite but may also be used separately. For example, if the eye facet model could be used in another rendering framework.

Most of the technical details of the implementation, which are omitted from the current manuscript for clarity, can be found in Jan Stankiewicz’s Master thesis, available on request.

Environment

This module controls the loading and use of the 3D models that compose the virtual environment. It has been developed to fit with Stürzl et al. [281]’s Laser acquisitions of naturalistic ant environments. These clouds of points are available on <https://insectvision.dlr.de/3d-reconstruction-tools/habitat3d> as meshes in ply format, which is an easy to use, plain-text format for representing three-dimensional meshes. The expected ply files should contain three arrays for, respectively, vertices coordinates (x, y, z in *float32*), faces composition (3 vertices IDs per face, in *int32*), and vertices colours (RGBA values, in *uint8*).

A ‘full’ mesh containing every visible element (ground, vegetation, objects, etc) should thus be provided, along another (possibly much simpler in geometry) ‘ground’ mesh. The

physics functions of the environment module can be thought of as a basic simulation of gravity for vertical projection of 2D coordinates (x, y) to the ground mesh's geometry, allowing the engine to position an agent anywhere in the world only using x and y points; see **Results** for more details and plans for upcoming features. In order to minimize the runtime performance footprint, this computation is performed with a KD-Tree [14] of the vertices IDs, allowing efficient identification of the closest face's geometry for any given (x, y) coordinate. The *cKDTree* function, from the Open-Source package Scipy is used, because of the performance provided by its C++ bindings.

Engine

The 'engine' module does the heavy-lifting graphics computation, by interpreting the 'environment' module's mesh data and generating the views. To that end, the selected approach is one that is widely used in computer graphics: rasterization. The rasterization technique is based on two main steps to convert 3D data into a 2D image. First, the point of view of the observer is computed using a virtual camera, of which viewpoint and projection are computed by transforming each visible vertex with three homogeneous transformation matrices (MPV method, for Model, View, Projection). Together, these transformations place a parameterised camera (view) in the virtual world (model) and apply a perspective projection in which nearby objects appear larger than distant ones. These transformation matrices are computed by the 'camera' class in the 'engine' module and are then used to project each primitive of the 3D space to the according 2D viewport.

OpenGL is selected for the rendering pipeline because it is fully Open Source and cross-platform. The PyOpenGL library, which provides Python bindings to OpenGL's C++ interface and GLSL language, is therefore used. This approach allows for direct rendering on the GPU, allowing parallel processing by the dedicated hardware, and alleviating the CPU's workload. This OpenGL pipeline is performed by the 'rendering' module of the 'engine' module.

The 'engine' module also comprises an 'actors' module which consists in agent-based objects, providing the principal interface with the user's custom code (see **Results** section for more details).

Insect eye model

Ommatidial response function

The performance of a single lens focusing light, from a standard photographic field of view, begins to deteriorate below a diameter of 4 mm [73]; spherical and chromatic aberrations prevent the ability to achieve the visual acuity that is required for the behaviours displayed by invertebrates. Nature’s answer to the problem is the compound eye, a structure that allows behaviourally useful visual acuity at the insect’s small scale by pooling multiple independent light detecting units, each typically with a narrow field of view. These units are called ommatidia and comprise of a lens and a cluster of sensing cells. Viewed normal to the surface of the eye, the aperture of each ommatidium is referred to as a facet and is generally circular or hexagonal in shape.

Each ommatidium only focuses photons from its particular acceptance angle A , resulting in a Gaussian-shaped sensitivity function [257]:

$$A = e^{-2.77(\frac{\theta}{\Delta Q})^2} \quad (1)$$

where θ is the angular displacement, ΔQ is the full width at half maximum of the rhabdom acceptance.

This function estimates the neural response of an ommatidium given the angular displacement θ , of a distant point source from the longitudinal axis of the ommatidium and is in most cases a close approximation for apposition eyes found in diurnal insects [145].

The compound eye model presented in this work thus gathers all of the virtual photons in each ommatidium’s viewing direction and averages them according to the angular sensitivity function (eq. (1)).

Parameterization of the ommatidia

Each facet forms a small aperture that accepts light from a narrow field of view, resulting in optical attributes of negligible distortion, chromatic/spherical aberrations, and an effectively infinite depth of field [260]. However, the aperture size is constrained by diffraction; a reduction in the diameter of a given facet increases the ommatidial blur. In the case of a compound eye with diffraction-limited acuity, ‘a doubling of resolution requires a doubling of the diameter of each ommatidium as well as a doubling of the

number of ommatidia in a row. The consequence is that the eye must grow as the square of the required acuity' [145, 136]. This implies certain evolutionary constraints on the adoption of the compound eye where high acuity is an evolutionary advantage and it is thus common to find in Nature that the dimensions of ommatidia vary across the surface of a given compound eye, in order to allow for zones of better acuity in behaviourally relevant portions of the visual field.

It was therefore important for the compound eye model presented in this work that the location of each ommatidia and its acceptance angle be independently tuneable by the user, and that for each unit the angular sensitivity function for three independent colour frequencies would also be tuneable. The parameter set, P , is outlined below:

$$P = \begin{pmatrix} \beta_1 & \epsilon_1 & \Delta\rho_1 & uv_1 & g_1 & b_1 \\ \beta_2 & \epsilon_2 & \Delta\rho_2 & uv_2 & g_2 & b_2 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_n & \epsilon_n & \Delta\rho_n & uv_n & g_n & b_n \end{pmatrix} \quad (1)$$

where β = ommatidium azimuth, ϵ = ommatidium elevation, $\Delta\rho$ = ommatidium angular acceptance function, uv , g and b = ommatidium spectral responses; and n = total number of ommatidia.

Implementation of the parameterized compound eye model

The compound eye model is implemented following Titus Neumann's method [198], that is to say, using a cubemapping approach. This approach was selected as it is based on the rasterization technique (see **Methods** paragraph **Engine**) and is therefore particularly suited to the OpenGL pipeline.

Briefly, the panoramic scene (360 degrees all around the agent) is rendered on six viewports that compose the six faces of a cube (each with a 90° field of view horizontally and vertically). After this cubemap is rendered, samples are taken for each ommatidia: a cone shape, with its apex on the agent's position, is projected onto the surface of the cubemap and the pixels within the cone boundary are included in the light intensity calculation for the current ommatidium. In other words, for a given compound eye model, each ommatidium maps to a set of pixels on the surrounding environment.

The angle (θ) between each pixel on the cube and the axis of each ommatidium is calculated using a vector dot product operation, and the contribution of each pixel to each ommatidial response is calculated using this theta and the angular sensitivity function

equation (eq. (1)).

The contribution from each pixel to the ommatidial response rapidly drops off beyond a certain angle. Thus, contribution weights inferior to 10^{-5} are set to 0, allowing the storage of the weights in a SciPy *CSC sparse matrix* [294]. These weights are then normalised such that the sum of all the weights for an individual ommatidia is 1.0.

The weights need not to be computed at each step and can persist as a lookup table for a given compound eye model; they are therefore computed just once, in the initialisation phase for each new compound eye model (and stored on disk for future simulations). Because each ommatidium's output is a precomputed lookup table of the cubemap pixels, the computational cost of rendering a scene six times (for each of the cube's 6 faces) is negligible, making the method amenable to scaling. This also means that the resolution of the cubemap faces (in pixels) plays an important role on the generation of the weight maps, and that it can be optimised for efficient processing (fig. 2.2).

Human output

The 'engine' module provides the possibility to display the rendered panoramic scene to the experimenter, using two techniques. One is the classical equirectangular projection, that maps a spherical image to a rectangle. The other, useful for visualising an approximation of what the compound eye model receives as input, uses a Voronoi visualization, where each ommatidium's viewing direction is converted into a latitude and longitude, so that it be plotted on a 2D surface. The module uses the approach outlined in Telea and van Wijk [284], which takes advantage of OpenGL's depth test functionality for the rapid generation of such Voronoi diagrams, allowing real-time visualisation of the compound eye simulations. The method is to draw a cone of equal proportions for every point in the dataset and translate the central axis of the cone to the required latitude and longitude of the data point, while keeping the bases of all cones lying on a common plane. When viewed from above with an orthographic projection, the OpenGL depth test ensures that each pixel of the 2D surface is rendered with the colour of the nearest (Euclidean distance) cone central axis. However, the time taken to render a frame scales linearly with ommatidia count which is problematic for rendering the vision of high acuity compound eyes in real-time.

Both these visualisations can be done in real time in agent-based models by use of the 'actors' objects, but it is worth to note that they are optional, as the rendered scenes may be also outputted directly as matrices for further use in the user's code.

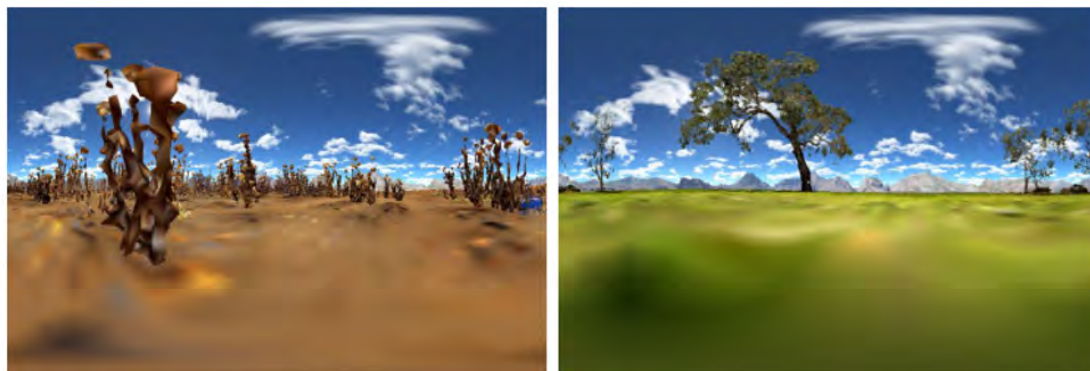


Figure 2.1: Snapshots of the panoramic rendering tool

Results

Environments

This module is used for importing the environment data into a Python dictionary containing the vertices coordinates, colours, the faces composition, and the KD-Tree (see **Methods**). In the current version of the package, only meshes in ply format are accepted; future updates will allow the import of additional formats, and potentially support for classic textures (2D bitmaps) for colours representation.

Full ply meshes to render should be accompanied by a mesh containing only the ground geometry, for computation of the vertical projection (See **Methods** section, and up to date information in the code repository).

The physics module will include, in upcoming iterations of the package, the handling of the agent's roll and tilt, for more accurate sensory-motor modelling.

Engine

'RegularActor' and 'InsectActor' objects represent the agent-based interfaces that the user may use with their custom code, by specifying a position in the world and grabbing the visual input from there. They can thus be used in the user's custom loop for navigating agents, or as standalone to grab a specific image from a specific point in the virtual world.

Real-time simulations are achievable with live display, in the virtual worlds cited above [281] in satisfying framerate (for instance, more than 60 fps for a RegularActor,

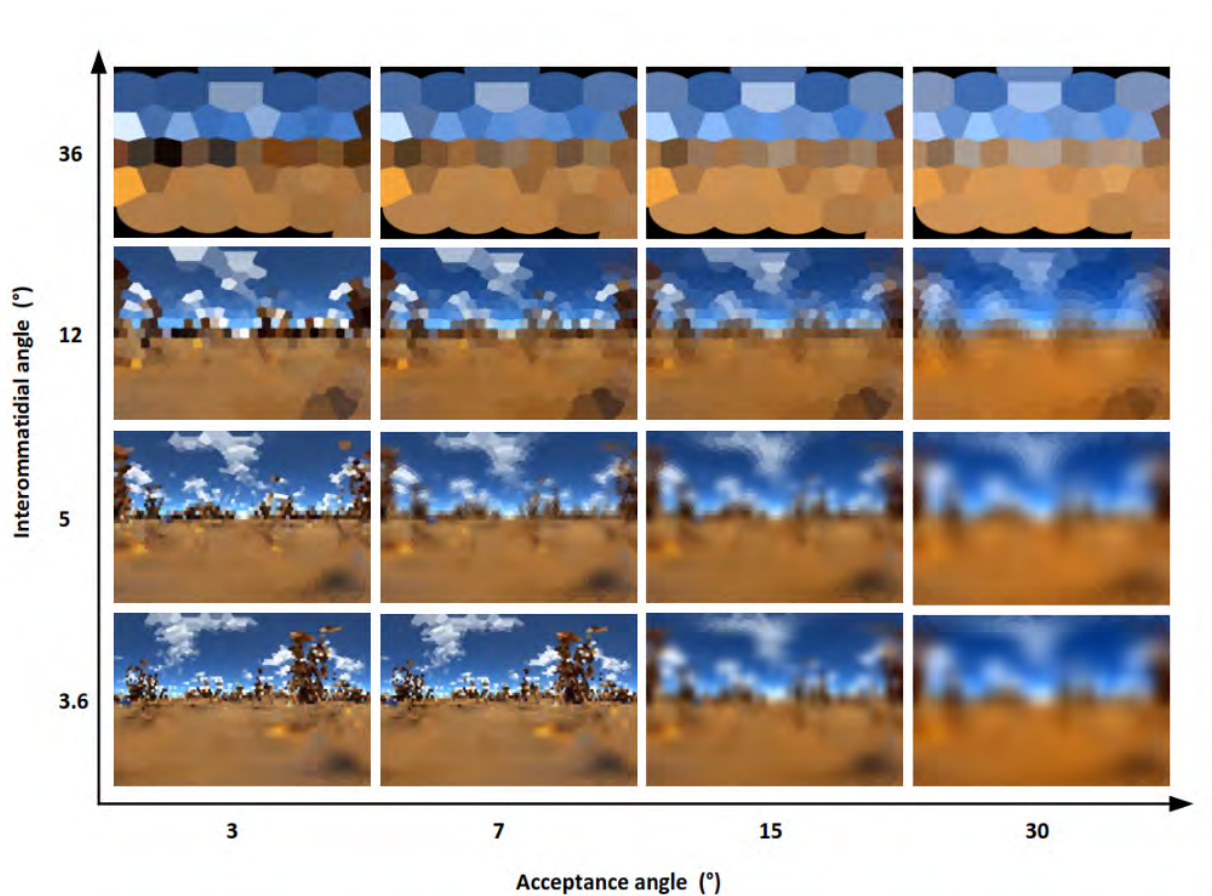


Figure 2.2: **Effect of the inter-ommatidial and acceptance angles**

30 fps for a 1900-ommatidia InsectActor, 15 fps for a 10,000-ommatidia InsectActor, on a consumer-grade GPU; Nvidia GTX 1080). Simulations without live display should provide better performance.

Insect eye parameters

The insect eye is fully parameterized (see **Methods**) and each ommatidium may be described individually, but it can also be generated from scratch (see below)

The output from the compound eye rendering tool is plotted for a range of uniform eye models. Fig. 2.2 indicates that as the interommatidial angle increases the resolution of the human interpretable output decreases. It is also apparent that an increase in the acceptance angle results in a blurring of the image.

Generation of a uniform insect eye from scratch

If the user does not provide a fully parameterized insect eye, it is possible to generate a uniform one from a passed number of ommatidia. The process is based on the subdivision of an icosahedron, where each vertex latitude and longitude correspond to the viewing direction of an ommatidium (consider each ommatidium as one face on the associated dual-polyhedron). The uniform eye is thus the approximation of a sphere, and each ommatidium covers a viewing angle inversely proportional to the number of ommatidia (i.e., to the number of subdivisions) so as to cover the whole 360° .

Discussion

A suite of Python tools is presented, that allows for real time behaviour-in-the-loop modelling, with the possibility to render insect vision through compound eye models. While able to load complex-enough meshes, a disadvantage that is common to all current vision-based simulations is that it is not yet possible to develop environments as rich as the real world. In general, simplifications are made so that simulation environments are optimised look real to the human eye, and information that is not perceived by humans is discarded. Therefore, recreating a realistic representation of the visual sensory experience of other organisms remains a challenging task [281]. Future development of the InsectVisionSimulator package should focus on a broader support for 3D meshes and textures and would also greatly benefit from the use of raytracing techniques (instead of rasterization), for realistic lighting and dynamic shadows, which may impact real-world visually guided behaviours. Making use of the more recent Vulkan pipeline (destined to replace OpenGL in the future) or rebasing the module on another abstraction layer such as the Open Source OGRE3D would be beneficial.

The parametrised model that can be tuned to represent a wide array of compound eyes, each with its own idiosyncratic ommatidial distribution, can have applications beyond behaviour-in-the-loop simulations. Analysis of the distribution of ommatidia and its effect on an organism's ability to perform visual behaviour could be useful in enhancing current neural models of perception, improving robotic vision algorithms, and shaping the next generation of artificial compound eye models. For instance, a process for deriving more accurate angular sensitivity functions that the Gaussian approximation could be thought of, as the one outlined in [265, 264, 266].

Conclusion

The aim is to share and provide a readily available solution to run fast vision-based simulations in complex worlds. InsectVisionSimulator improves greatly the rate as well as the accuracy at which views can be rendered in comparison to previous approaches. Its modularity and versatility make it a useful tool to various modelling applications, from the study of neural visual processing to complex sensory-motor dynamics, and the resulting behaviours emerging when in closed-loop with the environment.

Chapter 3

Visual pre-processing to facilitate the encoding of views in an insect Mushroom Bodies model

Florent Le Moël, Antoine Wystrach



This chapter is intended to be published.

Introduction

In the insect realm, central-place foragers such as ants or bees, spend most of their life in the nest, but there comes a time where they are faced with a great challenge for their survival and the survival of the colony: they must wander outside in search for food, and be able to bring it back home safely. Navigating through the complex world that lays beyond the bounds of their home is no easy task, but these animals, despite a very small brain, display remarkable abilities to do so.

In desert ants, there is a marked temporal, age-related polyethism [314]. The interior-exterior transition at the onset of these ants' foraging life is crucial [232]. When the adults leave their role as nurses and nest-confined workers [238, 314] and before actually venturing far away searching for food, the new foragers typically spend 2 to 3 days [70, 126] performing very stereotyped sequences of movements around the nest entrance called Learning Walks (LW). Such process serves to gather the necessary visual memories that will later be used for visual homing [199, 313, 192, 269, 70, 71, 72, 89, 46, 126, 280, 187]. In addition to the learning of these nest-centred views, desert ants are also known to be able to visually learn and follow idiosyncratic routes within their foraging territory [140].

Even if it is still not completely clear how these views are learnt, stored, or used for an actual navigation task, the increasing progresses in the description of the insect neural circuits start to shine light on the matter. Indeed, there is now direct evidence that the Mushroom Bodies (MB), a pair of prominent and evolutionary conserved neuropils, are required for view-based navigation in ants [128]. More specifically, impaired MBs cause defects in the use of learnt views but not in the innate response to visual cues [24], suggesting an important role of the MBs in learning and memory for navigation.

How the MBs neural circuits can encode memory has been mainly studied in the context of olfactory learning in flies and bees [207, 30, 283, 106], but way less in the context of visual learning [143, 270, 66]. The main characteristic of the MBs is the sparse encoding happening there [207], across the thousands of intrinsic 'Kenyon Cells' neurons (named after Kenyon [131]). The axons of these Kenyon Cells represent the bulk of the MB structure, while their dendrites compose the MBs' Calyces - the main input region - [107, 106] their terminal axons compose the MB's lobes - the output regions. The Calyces of the MBs can be segregated in three subregions receiving respectively olfactory input, visual input, or both [174, 90, 69].

Interestingly, the volume of the MBs and of the visual input areas in the Calyces has drastically increased in Hymenoptera that have a nest where they need to come back to, suggesting that the ability to store complex visual memories may have allowed the evolution of central-place foraging in these species [232, 68]. Multiple evidence, such as

in *Cataglyphis* ants [92] shows the existence of optical tracts (optical calycal tract (OCT) and anterior superior optic tract (ASOT)) projecting from the Medulla and Lamina of the Optic Lobes to the Calyces of the MBs. The ASOT has only been observed in several Hymenoptera so far [62, 173], whereas the OCT has only been described in *Cataglyphis* [92].

Remarkably, the MB circuitry - modelled at first [106] for olfactory learning – turns out to be perfectly suited to also encode visual memories for navigation [5, 300]. Notably, Ardin et al. [5] present a bio-plausible model of the MB sparse encoding that is able to store multiple images learnt along routes in a virtual environment and to distinguish previously seen images from novel ones. In this model, visual information is sent directly to the MBs. This contrasts with reality, as visual information in insects transits through several neural relays before reaching the MBs, notably in the Optic Lobes (OL), which are themselves composed of relays in the Lamina, the Medulla [62, 92] and optionally the Lobula and Lobula plate [151]. The exact nature of the different types of processing happening along these relays is still unclear, and how these could actually serve (or harm) navigational performance is entirely unknown.

Our aim is here to use a computational approach to investigate how biologically relevant visual processing can impact the encoding and retrieval of visual memories in the MB. We present a MB-inspired bio-plausible model, but with added biological constraints upstream of the MBs. Specifically, we explore the effect of known mechanisms such as colour opponency [177]; lateral inhibition between neighbouring ommatidia in the lamina and medulla [262, 125]; the pruning of Projection Neurons to KC connections known to happen upon the beginning of foraging life [233, 26]; and the input connectivity and sparsening activity of the KCs [152].

Overall, this works show how these added processing are key for the learning of long routes in a complex 3D environment and allow efficient visual navigation at very little computational cost.

Methods

3D Environment

To investigate how the MB circuitry can encode visual memory for navigation, a virtual environment accurately reproducing visual characteristics of real natural scenes was needed. To this end, we used a dataset generated by the software Habitat3D [226]. This open-source tool provides photorealistic meshes of natural scenes, from point clouds ac-

quired with help of a LiDAR scanner (IMAGER 5006i, Zoller+Fröhlich GmbH, in the case of the dataset used here) [281]. The point cloud used here is mapped on a typical natural habitat of ants, represents an area of about 30 meters radius, and features large eucalyptus trees and several smaller vegetation items. This dataset can be found on the Insect Vision webpage (<https://insectvision.dlr.de/3d-reconstruction-tools/habitat3d>). The original high-resolution mesh has been down-sampled with the open-source software Blender [48] and exported as vertex matrices in Polygon File Format where each vertex is defined by its 3D coordinates (x , y , z , in meters) and a colour encoded in Red, Green, Blue values. We ran the simulations with help of our *InsectVisionSimulator* tool (chapter 2) that allows for running 3D OpenGL-based simulations in Python, using such environment meshes. The tool also provides an *insect eye* camera (see chapter 2 or below for a quick overview), we embedded in an agent-based model allowing to capture views in different positions in the world, or along routes.

For the agent’s displacements, we only consider the horizontal (x and y) axes, with the third (z) axis being calculated at all times by vertical projection onto the mesh under the agent. In other words, the viewpoint follows the ground topography as if it hovers it at a constant height (fixed for the present work at 3 cm). Also, we only consider here change in yaw rotations, not pitch and roll. The impact of latter two on the use of view could be considered in future study. Non-ground elements (i.e., vegetation) are walk-through. The sky has no texture in order to facilitate the distinction between sky and ground (as can be achieved by navigating insect using the UV-green channels opponency [118] and has been replaced by a uniform blue colour (see section *Colour processing*).

Insect eye model

Visual input from the virtual world is acquired through a 3D model of the insect faceted eye (chapter 2). This faceted eye model is generated via subdivision of an icosahedron, where each vertex latitude and longitude correspond to the viewing direction of an ommatidium – or one Lamina cartridge (consider each ommatidium as one face on the associated dual polyhedron).

In this work, just like the crystalline cones of the ommatidia focus photons from a particular viewing angle (i.e., ‘acceptance angle’) onto the rhabdoms [121, 298], each modelled ommatidium covers an acceptance angle and pools all pixels from the given region. We set here the acceptance angle to approximate the interommatidial angle in order to sample the full visual space. In other words, the acceptance angle is inversely proportional to the number of ommatidia (i.e., to the number of icosahedron subdivisions). We fixed the number of ommatidia for all experiments to 162 (this corresponds to 5 subdivisions of an icosahedron). Consequently, each ommatidia covers a viewing angle

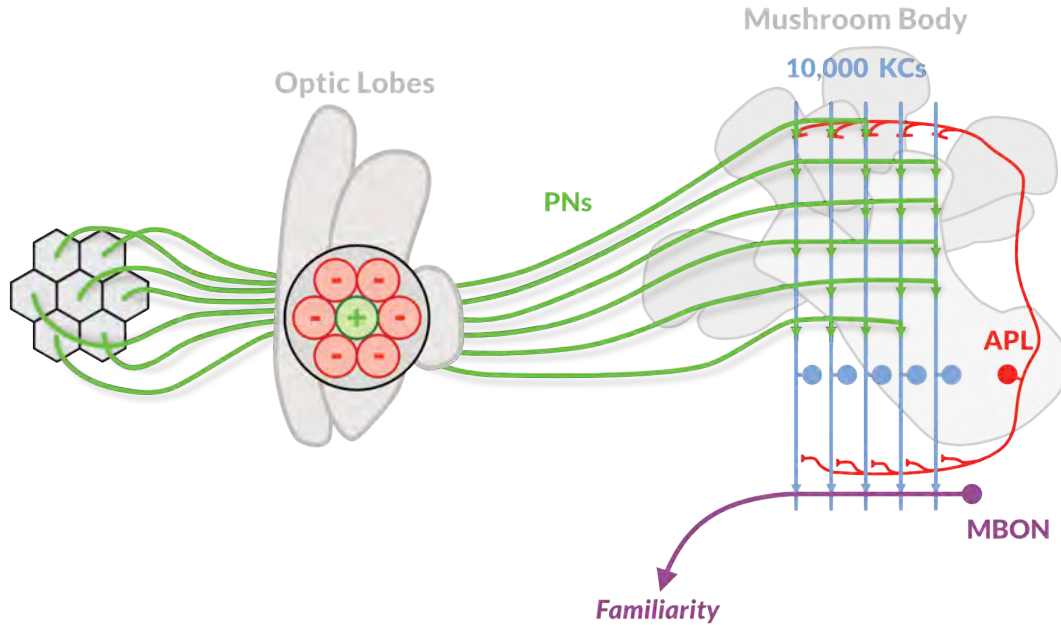


Figure 3.1: Model overview

of 18.0° and takes as input the three colour channels of the OpenGL-rendered 3D environment (Red, Green and Blue colour channels), each being encoded in values between 0.0 and 1.0.

Insect brain model

Similarly to the other typical MB models, the ommatidia/cartridges (see ‘Colour processing’ section) act as the input space, the Mushroom Body intrinsic neurons (KCs) as the high-dimensional space, and the Mushroom Body Output Neuron (MBON) as a linear classifier (fig. 3.1).

Neurons activation functions and Synaptic weights As our aim in the present work is not to model the neural response dynamic at a cellular level, but rather to investigate the interplay between multiple larger-scale biological processes, we chose not to model the membrane potential nor the sinusoidal response of our neurons. Instead, the PNs are encoded as simple firing rates ($[0.0, 1.0]$ interval), with additive integration for the excitatory postsynaptic potentials (ePSP) in the KCs dendrites. However, the KCs’ actual firing activity is encoded as binary values (logical 0 or 1). Indeed, KCs are known to fire only rarely and timely: usually one action potential at a key timing during the Local Field Potential oscillatory rhythm [146]. This suggests that they act similarly to a binary

value population code, justifying the need to constrain our model to a binary encoding of whether a given KC spikes (1.0) or not (0.0), rather than to continuous values.

Synaptic weights in our model are fixed, with the exception of the two layers where some form of learning may happen: the PN-to-KC synapses, and the KC to MBON synapses. In both cases, these synapses follow a binary, instantaneous weight change (initialized at +1.0, fully excitatory; set by learning to 0.0, in one shot). This simplification enables us to ensure the effects observed are not dependant on a gradation of synaptic weights, where models can be infinitely accurate (beyond biological reason).

Colour processing

Both in the retina and the optic lobe, a columnar organisation is preserved (retinotopy). In the Lamina, these columnar units are called ‘cartridges’. Each cartridge receives input from the central receptors of the overlying ommatidium and from the surrounding receptors of neighbouring ommatidia. Thus, a given cartridge receives input from a small group of ommatidia that are all pointing towards the same direction in the visual field [160, 120, 221, 220, 222].

As in seemingly most ant species, we assume that our agent has two receptor cell types: so called UV-receptor and Green-receptor [182, 2]. Assuming that the sky’s global irradiance represents naturally the major source of UV light [27], we render in our simulation the sky as uniformly blue and use the blue and green channels from the render to activate the agent’s UV and green receptors respectively. Thus, the first component of our model converts the RGB values from the 3D rendering (chapter 2) that each ommatidia receives, into a single output firing-rate, therefore approximating both the non-opponent achromatic luminance detection in the Lamina and the colour-opponent (subtractive) detection in the Medulla [180, 239, 108]. We look at two different UV-Green colour opponency, for Green dominancy (eq. (1), left), or the UV dominancy (eq. (1), right):

$$C_{rate_i} = \frac{(G_i - UV_i) + 1}{2} \quad \text{or} \quad C_{rate_i} = \frac{(UV_i - G_i) + 1}{2} \quad (1)$$

where G_i is the green receptor value of ommatidia i (and UV_i for UV receptor i), C_{rate_i} is the single firing rate value of cartridge i . Note that we refer to this input space using ‘ommatidia’ or ‘cartridges’ terms undifferentially in this work.

Lateral Inhibition

Lateral inhibition is very common in the sensory systems [262] is usually assumed to be implemented in a temporal fashion in the Lamina, using the delay in the co-incidence of a stimuli between two adjacent receptors [125]. Examples of biological applications of it include orientation selectivity, and feature detection [17]. Here, we circumvent the non-linearity that is typically associated with such visual processing [301] and directly implement our lateral inhibition like so:

$$PN_i = C_{rate_i} - \left(\sum_{n=1}^6 C_{rate_n} \right) \times \frac{1}{6} \quad (2)$$

where PN_i is the total input to the PN i and C_{rate_n} are the firing rates of the $n = 6$ neighbouring cartridges for cartridge i .

Projection Neurons layer

The output of each cartridge after colour processing and additional processing (see paragraph **Lateral Inhibition**) is conveyed by a layer of visual Projection Neurons (PN) to the MB. This layer is composed of as many neurons as there are of cartridges. Before learning, the output synaptic weights (onto KCs) are all set to +1.0, so the output of this layer onto the KC dendrites is directly proportional to the excitation of the PNs for any given view.

Kenyon Cells layer

The Mushroom Body model is similar in its overall structure as the one in Ardin et al. [5]: this layer is composed of a rather large number of Kenyon Cells, set for most of the experiments (unless otherwise indicated) to 10,000 KCs. This represents an underestimation compared to real ants [92], but enables reasonable computation times with, while remaining conservative about memory space. The PN-to-KC connectivity pattern follows a pseudo-random rule where each KC receives a fixed number of inputs from randomly chosen PNs if and only if their output synaptic weights are not 0.0. Conversely, all PNs will connect in average to the same number of KCs. This connectivity scheme provides the fan-out pattern that is essential to the sparse encoding [146, 9]. Following the additive integration approach, each KC's dendritic ePSP will correspond to the sum of the inputs it receives: all the PNs activity that synapse onto the KC. This would normally require re-normalization of the values to fall into the [0.0, 1.0] range with help of an activation

function, however this is not needed here: whether a KC will fire an action potential or not (0.0 or 1.0) depends on the population activity of KCs and on the sparsening activity of the APL neuron (see **APL-like** paragraph).

Projection Neurons pruning

We add an approximated learning walk in the virtual environment, during which views are acquired from random positions contained in a circular area around a fictive nest. Then, we take the standard deviation of the activity for each PN across these learning walk views and compare it to a threshold. This threshold is the mean of the standard deviation values for all PNs. Every PN which falls under threshold is tagged for pruning. Then these PNs are eliminated, and the pseudo-random connections are regenerated, approximating what happens biologically (see **Discussion**).

APL-like normalisation and sparse encoding layer

We model the APL-neuron equivalent (APL in drosophila [152], A3-v in honeybees [53, 234], that acts as a filter: this neuron has been shown to act by applying an inhibitory feedback to the whole KC population, of a strength that is proportional to the sum of the inputs coming from the same KC population [152]. This results in a *winner-takes-all* selection of the most active KCs for production of a spike. We implemented this normalization in a relative fashion, where a defined portion of the KCs with the highest ePSPs get selected. Each selected firing KC can thus be coded in a binary matrix (1 = spike, 0 = no spike).

KC-to-MBON plasticity

Prior to any learning, all the KC to MBON synapses are set to their maximum value (+1.0), so that given additive integration, the firing rate of the MBON is equal to the proportion of selected KCs. The output value of the MBON therefore can be interpreted as representing an ‘unfamiliarity value’ for the current view, which is at first equal to 1.0. In other words, prior to learning (and as expected), any scene appears totally unfamiliar to the model.

During learning, the output synapses of the active KCs are inhibited (their weight goes from +1.0 to 0.0). Thus, after learning, if a familiar scene is presented again, the same KCs will fire again, but their synapses to the MBON will have been set to 0.0, meaning that the output of the MBON will be 0.0, that is, the view will appear familiar. Any view that will be somewhat similar to a learnt one, even not identical, may thus

activate a similar pattern of KCs and thus produce a familiarity that will vary between 0 or 1.

Results

In order to characterize the effect of known visual pre-processing (lateral inhibition between signals of neighbour ommatidia, pruning of the projection neurons) on the encoding and use of view for navigation, we look at the change in activity of the MB input layer (PNs activity) (fig. 3.2) and the model's familiarity output (MBON activity) along elementary displacements of the agent in the virtual world (fig. 3.3). These elementary displacements are of two types: either rotational, where we look at the change in neuronal activity between a reference position and a full 360° rotation on the spot, taking a view every 5° (fig. 3.2a, fig. 3.2c, fig. 3.3); or translational, where we look at the change in neuronal activity between a reference position and a set of 40 increasingly distant positions (on a log space) in a random direction (fig. 3.2b, fig. 3.2d, fig. 3.3). For this experiment, the MB model is set with 10,000 KCs; each KC receives input from 25 random PNs; and the APL normalisation enables 1% of the most excited KCs to fire an action potential. But as we will see, the insight resulting from this investigation is independent of these parameters values.

First, in the input layer (PNs) (fig. 3.2), we look at the difference in the response profiles in absence and in presence of lateral inhibition between the signals of neighbouring cartridges: without lateral inhibition, the PN layer response follows a rather classical rIDF profile [279, 344], with some amount of similarity extending up to 160° around the reference position (fig. 3.2a, fig. 3.2c). With lateral inhibition, we observe a sharpening of the rotational selectivity of the response: the PN layer's response shows similarity for only 60° around the reference position (30° on both sides). This effect is not surprising, as the centre-surround antagonism provided by lateral inhibition is known to increase the ability to discriminate [156, 320]. Results are similar for the translational movement (fig. 3.2b, fig. 3.2d): lateral inhibition sharpens discrimination in the sense that the similarity of the PN layer's response changes more quickly across displacement and reaches the maximum discrimination quicker than without lateral inhibition.

But it is by looking at the MBON familiarity output (fig. 3.3) that we can observe the key importance of early lateral inhibition. Without lateral inhibition, the maximum MBON activity stays around 0.5, meaning that, at the MBON level, completely different views (such as the ones 180° opposite of the reference one) still appear 50% similar to the reference one. This value drastically improves with the presence of lateral inhibition: the model can fully differentiate between the reference view and other views. This observation is also true for the translational experiment, where the presence of lateral

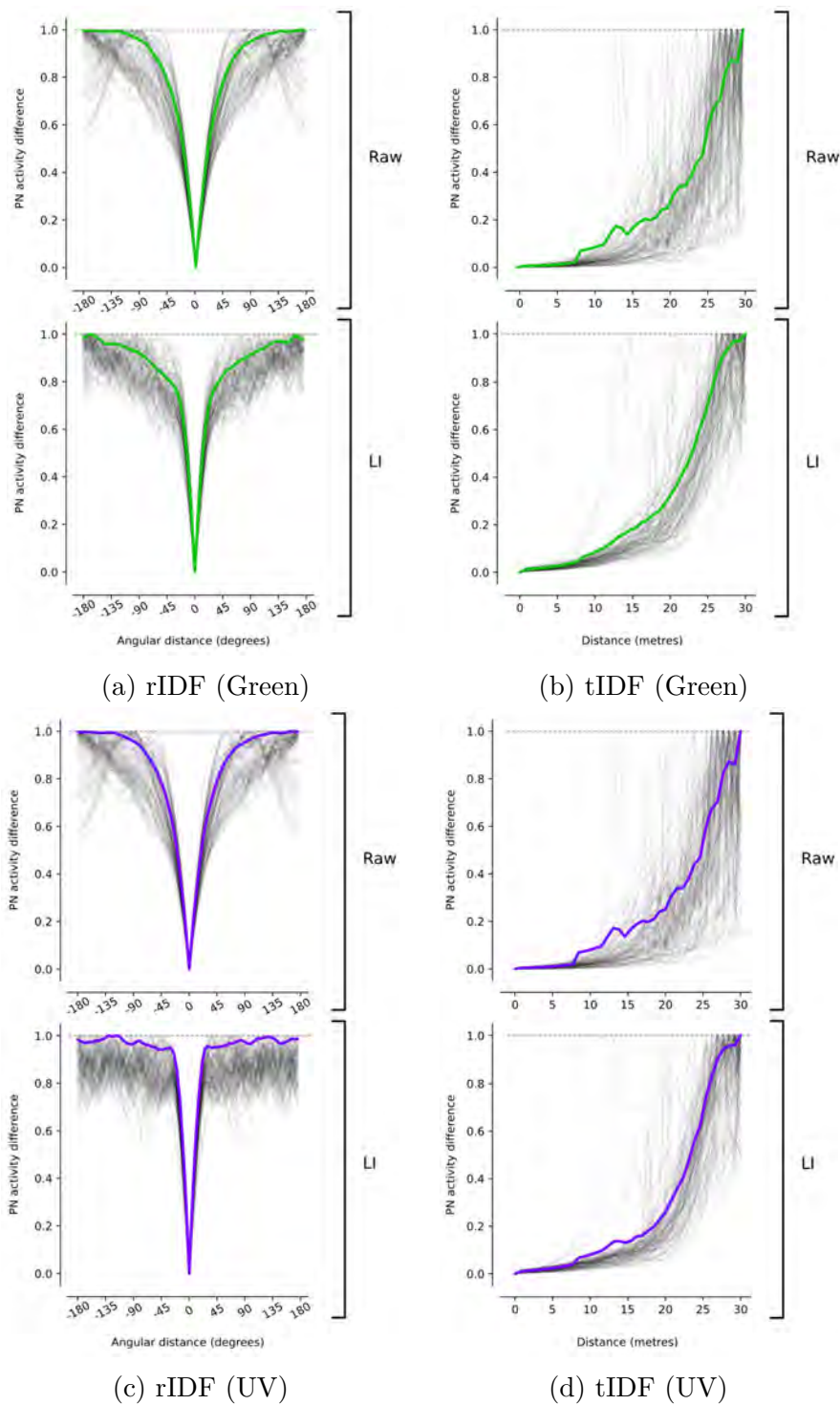


Figure 3.2: **PNs Image Difference Functions**

Difference between a reference view and the other views along either a rotation in place (*a*, *c*) or a linear displacement (*b*, *d*). *Raw*, raw image; *LI*, With lateral inhibition. *a*, *b*, Green dominance (*Green-UV*); *c*, *d*, UV dominance (*UV-Green*).

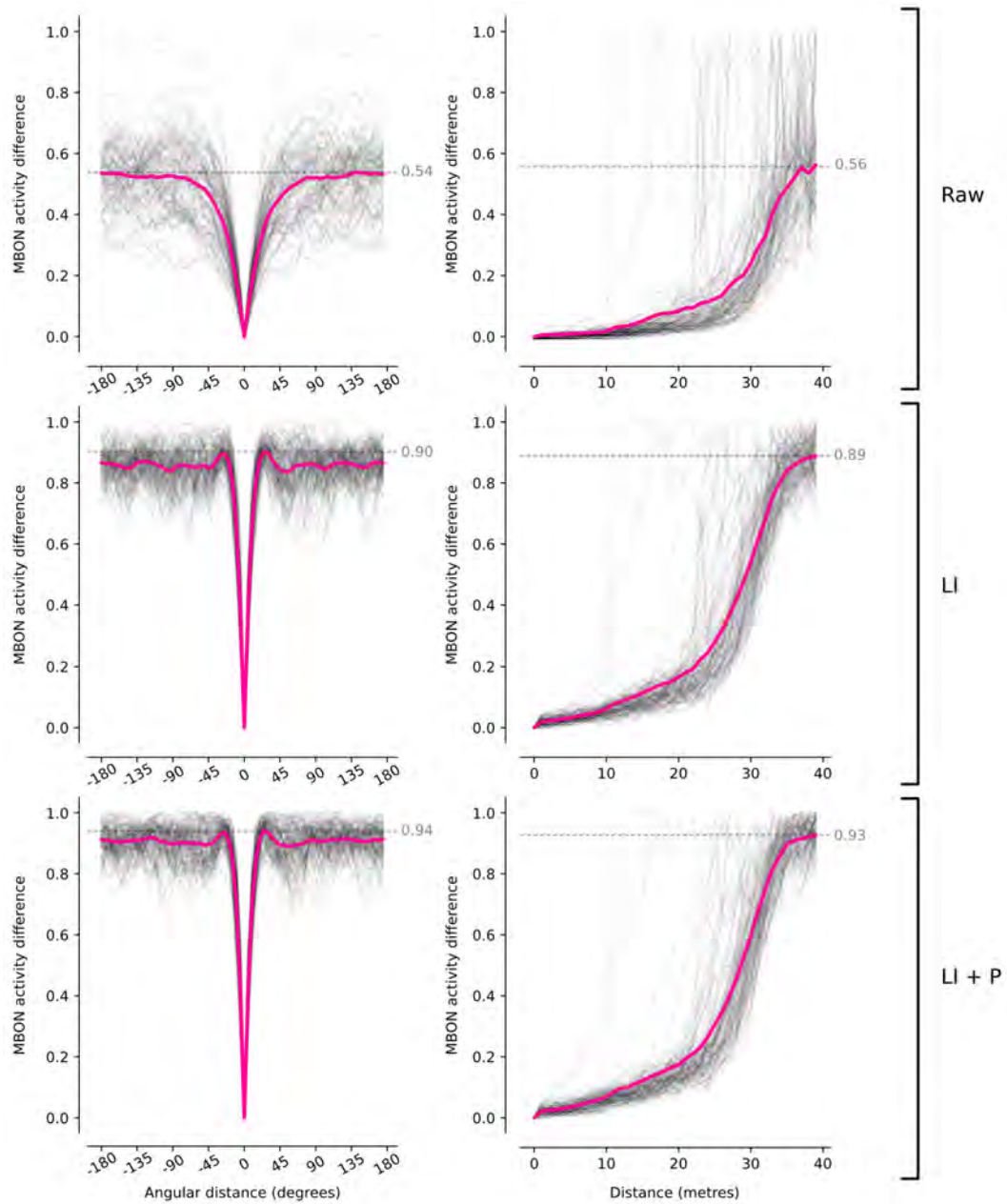


Figure 3.3: **MBON Difference Functions**

Difference between a reference view and the other views along either a rotation in place (*left*) or a linear displacement (*right*). *Raw*, raw image; *LI*, With lateral inhibition; *LI + P*, With lateral inhibition and after pruning.

inhibition bumps the discrimination ability from 56% to 89% after 35 m. In a sense, lateral inhibition as observed in the Lamina of insects [167, 125, 119] is strongly improving discriminability between familiar and unfamiliar views in the MB. The mechanistic reason will be investigated subsequently.

The addition of the pruning of projection neurons further improves the discrimination range in the MB, but its importance will appear more clearly in the following experiments.

We know that in the MB, only the KCs receiving the strongest inputs (highest ePSP) will fire a spike and transmit information about the current scene further. Therefore, it is important that in the PN layer, the PNs that fire strongly actually carry useful information for scene discrimination. Whether a PN is discriminative or not (that is, whether it carries useful information about the scene's identity) can be simply quantified by looking at the standard deviation of the PN's response across displacement along a route: the higher the variation in time, the more information it carries about the identity of the view experienced. Indeed, if a given PN's activity remains constant across displacements, it carries by essence no useful information for recognising locations. We therefore observed the variation of activity of the PNs along a random walk in the virtual world, in relation to their average activity (fig. 3.4).

This repartition of the PNs activity shows important clustering of the response profiles. Like in the Medulla, each PN we modelled responds to a specific zone of the visual field, and thus can be associated to a corresponding latitude and longitude in the panoramic scene where the ommatidia points. We can thus identify clusters of PNs responding to the region of the sky; the ground; the upper horizon; the lower horizon (fig. 3.4c). As expected, the PNs responding to the region above the horizon carry the most information about scene identity, because this is where most of the change in panorama happens due to the relative movement of the trees and bushes. However, we observe that without lateral inhibition, there is no clear relationship between the average and variation in activity of PNs. The most active ones do not necessarily carry information allowing scene recognition (see fig. 3.4a, fig. 3.4b). For instance, PNs responding to UV receptors (*UV – Green* opponency) (fig. 3.4b) are most strongly activated in the region that points to the uniform sky area, meaning they're uninformative for scene recognition. The problem is even starker when considering the green receptors (*Green – UV* opponency), as seen with the poor vertical separation of the clusters in fig. 3.4a. Without lateral inhibition, the most active PNs – the ones that will contribute most to the KCs' activity – are pointing below horizon, that is, a region that carries little information to discriminate scenes reliably. In this virtual world (like in reality) the most informative region corresponds to the above horizon (fig. 3.4c). The addition of lateral inhibition enhances the vertical separation of the clusters, silencing the least informative PNs that point in visually unchanging regions, and enhancing the response of the informative PNs that detect contrasted edges, which

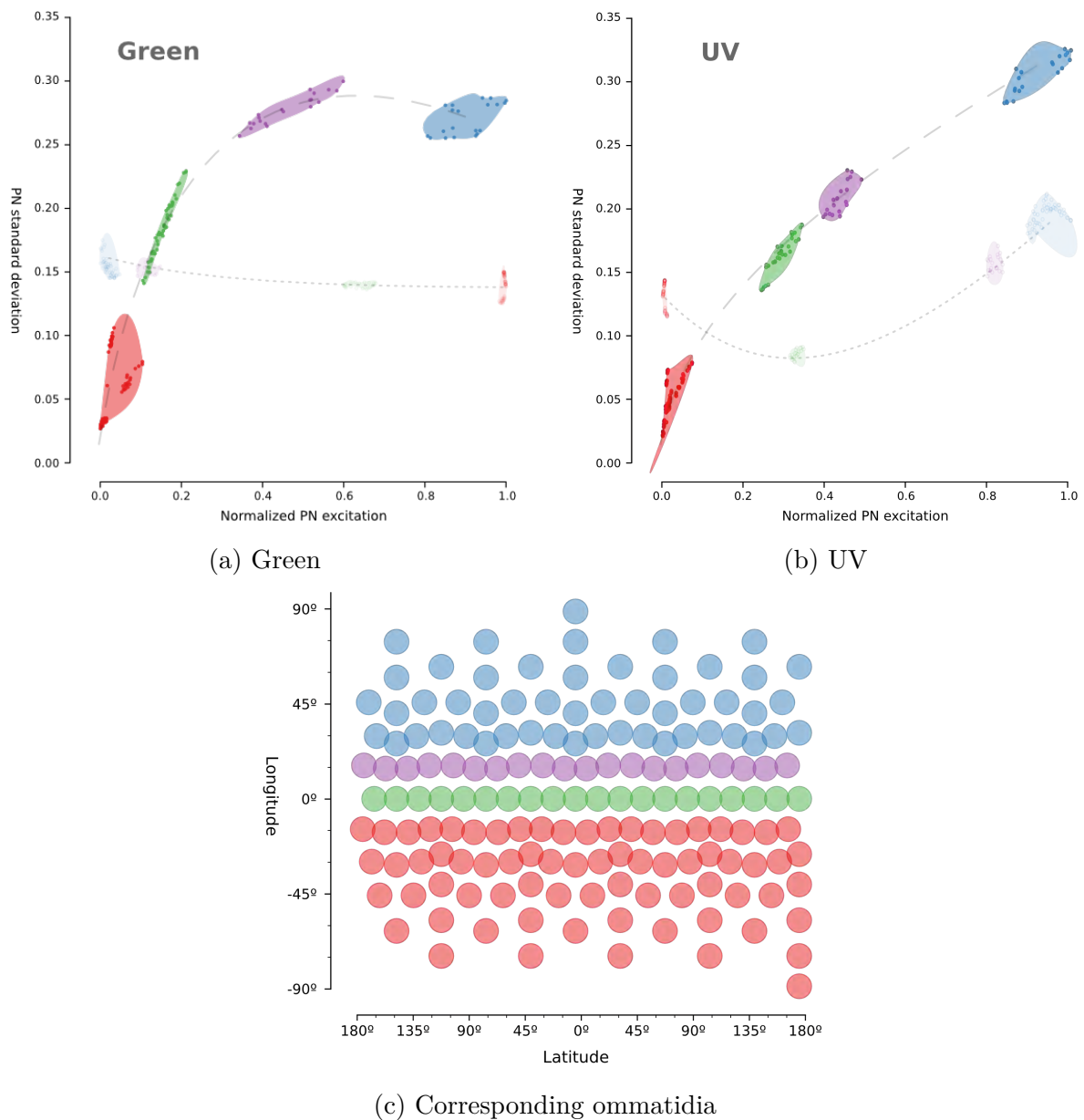


Figure 3.4: **PNs informativity**

PNs activity along random routes, in relation with the standard deviation of that activity. A high *sd* means the PN firing profile varies a lot; a low *sd* means the PN rarely fires or always fire. *a*, Green dominance (*Green-UV* opponency); *b*, UV dominance (*UV-Green* opponency); *c*, Corresponding ommatidia directions for each cluster in *a* and *b*. In *a* and *b*, Transparent points and clusters (and dotted line): Raw image; Opaque points and clusters (and dashed line): after Lateral Inhibition.

will vary across displacement and thus carry information for discriminating scene.

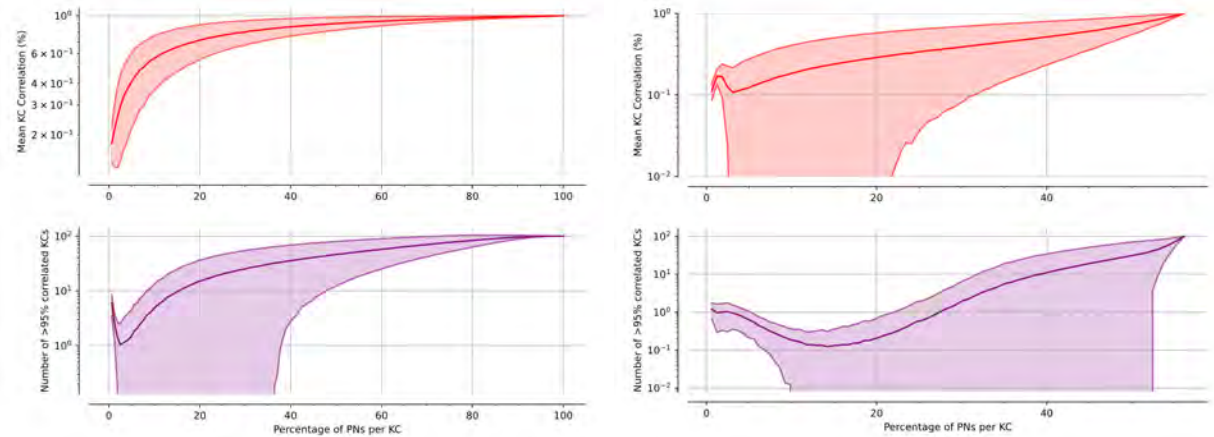
In our simulations, the opponency between $UV - Green$ or $Green - UV$ result in very similar information to that of UV and $Green$ taken alone. This opponency might however be useful to cancel illumination intensity variations across the eye [55], but this was not required here given the constant light intensity in our virtual environment.

We then investigated the effect of the PNs-to-KC connectivity on the efficiency of the KC layer to discriminate across different locations along a long route. We look at the variation in the input profile of the whole KC population across multiple random routes, for all possible number of PNs per KC (i.e., from 1-PN-per-KC, to all-PNs-per-KC) (fig. 3.5). For each PN-per-KC condition, we run 30 individual random routes of 500 steps, 5 mm per step. The MB model used in this experiment was limited to a number of 1,000 KCs for speed purposes, but this bears no qualitative effect on the results, as the connectivity effect is function of the ratio of PN to PN-to-KCs connections, and 1,000 KCs provide a good enough resolution for this endeavour. For each possible connectivity, we quantify whether the KCs' inputs profiles along the route tend to correlate across using a Pearson correlation coefficient across all possible pairs of KCs. This enables us to quantify the proportion of these cells that are redundant. Indeed, one expects an optimal system to tend to the lowest number of correlated KCs. Fig. 3.5 shows the mean correlation coefficient across the 1,000 KCs, as well as the total number of KCs that are correlated more than 95% of the time. According to combinatorics and given by a binomial coefficient, the maximum number of possible PN combinations that KCs could randomly sample is reached when each KC samples half of the existing PNs [127]:

$$K(m) = \frac{m!}{n!(n-m)!} \quad (3)$$

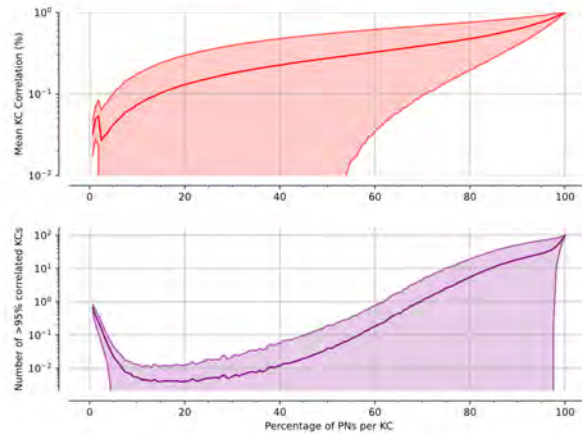
where K , the number of possible different PN combinations that KCs receive is maximum for $m = n/2$ if each KC samples m PNs out of n .

Contrastingly in our simulation, we observe that the optimal ratio of PNs per KCs connections falls to much lower values: between 2% and 5% of the PNs without lateral inhibition (fig. 3.5a), and between 10% and 20% of the PNs with lateral inhibition (fig. 3.5b). With the pruning of PNs, the number of KCs firing in correlation rises slightly (particularly visible on the mean correlation curve in fig. 3.5c, top): this is due to the fact that less PNs overall synapse to the KCs population, diminishing the absolute discrimination power of the system. However, the trade-off in terms of PN per KC connectivity remains the same. The reasons and consequences of these results will be discussed below.



(a) Raw

(b) Lateral Inhibition



(c) Lateral Inhibition + Pruning

Figure 3.5: **KC layer correlation**

Correlation of the KCs firing profiles (10,000 KCs) along random routes (3 m), in relation with the number of PN's-per-KC synapses. *a*, Raw image; *b*, With lateral inhibition; *c*, With lateral inhibition and after pruning. *Red*, mean correlation; *Purple*, Number of KCs correlated more than 95% of the time.

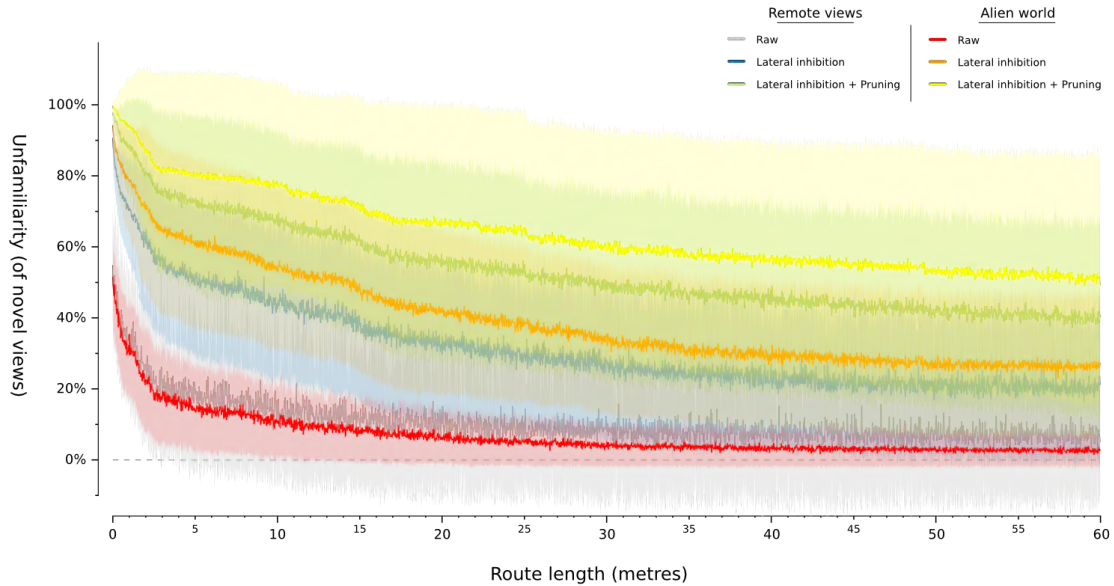


Figure 3.6: **Memory saturation**

Apparent unfamiliarity of novel views as the model learns long random routes (60 m). *Remote views*: novel views in the same world; *Alien world*: novel views from a differently structured world.

In order to observe how much memory space our MB model could provide, we observed the risk of ‘aliasing’ in the familiarity output as a function of the length of a route learnt (fig. 3.6). To that end, we made the agent learn progressively longer routes in the environment (from 0 up to 60 metres), while continuously testing its ability to discriminate between familiar and unfamiliar views sampled either at very distant position in the world (‘remote views’) or in a completely differently structured visual world (‘alien world’) (fig. 3.6). This allows to assess how ‘mistakenly familiar’ novel views appear as the model learns an increasingly longer route. If the memory space were to be completely exhausted by learning (e.g., all KC-to-MBON synapses set to 0.0), any new view, no matter how novel, would thus appear as familiar. Fig. 3.6 shows that with direct ommatidial activity input to the MBs, the unfamiliarity of novel views decreases sharply with the length of the learnt route (irrespective of whether these novel views were taken from the same world or the alien world). Novel views appear more than 85% familiar after the model has learnt a 10 metres long route only (fig. 3.6, gray and red curves). In contrast, with the lateral inhibition added, and after the pruning of PNs-to-KCs connectivity, the novel views can be identified as unfamiliar (>50% unfamiliar) even after learning a 60 metres long route (fig. 3.6, green and yellow curves).

Discussion

The MB is not made to accommodate raw ommatidial input

We show that the sparse coding present in the MB circuitry is well suited to encode, store and compare views, and that it allows for navigation in complex environments, similarly to Ardin et al. [5]. However, we show that sending visual information directly from the ommatidia – the ‘raw view’ – to the KC population suffers from severe aliasing, quickly exhausting memory space. This problem does not result from an absence of information in the ‘raw view’, but instead arises in the transfer from the ommatidial input layer to the high dimensionality code in the KCs layer. As only the KCs that receive strong PN inputs are likely to fire, a desired outcome would be that the PNs that fire strongly (and thus excite the KCs the most) should be the ones to carry navigation-relevant information. This is not the case in the raw view, where the PNs corresponding to the UV-intensive sky (high up above horizon) and green-intensive ground (below horizon) are the ones that fire the most. These two regions present few variations across different locations, and thus many KCs fire similarly across many locations – they are therefore useless for navigation.

Lateral inhibition ensures PN activity carries information

Remarkably, this problem is simply solved with the addition of lateral inhibition in the input of the PN layer. This process is well-known in early visual processing in the Lamina [156, 125, 119]. The usual observation of the role of lateral inhibition in compound eyes is multiple. For example, it can improve the angular sensitivity of the eye (i.e., it sharpens the image) [156], allowing better discrimination of the views, as seen in the rIDF profiles. Or it can act as an elementary filter for edge extraction [119] (akin to a Haar-like feature detector [91], which are classically used in machine vision applications [293]). It can also serve for feature (target) extraction or movement perception [17].

These roles of the lateral inhibition may indeed be advantageous for image processing in general, but the benefits we aim to highlight here are of a different nature and directly depend on constraints in the ways MB function. Early lateral inhibition does not so much improve the amount of information available in the PN layer (fig. 3.4) but enables to adapt the code mediated by the PN layer to ensure that this information will be carried out in the downstream stage of the KCs. Only the most stimulated KCs will fire an action potential, therefore, it is of great importance that the PNs that carries information for discriminating a scene at a given time are the ones that fire the most. By ensuring that PNs respond to the presence of contrasted edges in the receptive field, lateral inhibition

ensures that the strongly firing PNs carry information that necessarily changes across locations – information that is therefore relevant for navigation. This in turns enables the KC layer to convey relevant information as well, making the MBON classifier to be fully exploitable.

In the absence of lateral inhibition, many KCs fire in response to inputs from PNs stimulated by non-informative regions of the eyes. Thus, the effective pool of useful KCs is strongly reduced, and memory load is lowered. Impressively, the simple addition of lateral inhibition enables a huge improvement (fig. 3.6) of the length of the route that the agent can learn before saturating its own memory.

Pruning of PN-KC connections during early learning walks improves the system

However, with lateral inhibition only, some KCs still appear to fire in an uninformative fashion: either they fire most of the time, or never (fig. 3.4). Even if PNs respond to the presence of contrasted edges, due to the random connectivity, some KCs may end up receiving exclusively high-firing PNs, or rarely firing PNs, making them all that much uninformative as well.

It has been shown that the transition associated with the polyethism from nest workers to foragers in *Cataglyphis* ants resulted in important neuronal plasticity in the visual input synaptic complexes (micro-glomeruli) of the MB Calyx [255, 270]. This neuronal plasticity corresponds to a reduction of the micro-glomeruli density: an increase of the overall Calyx volume associated with a decrease in the number of micro-glomeruli. This decrease in density of (presynaptic) visual projection neurons is associated with a dendritic outgrowth of the (postsynaptic) Kenyon Cells in the MB Calyx [255, 270]. In other words, the onset of foraging triggers the axonal pruning of the visual projection neurons. Importantly, this is independent of the ant’s age and requires several days of light exposure, suggesting that these changes happen during the early Learning Walks period displayed by these ants, and are helpful for preparing the visual pathways to the impending navigational tasks [269].

Remarkably, we show that adding a simple pruning rule (see **Projection Neurons pruning** paragraph) after a learning walk does effectively further improve the effective memory capacity. Literally, this pruning can be viewed as an adaptation of the eyes to the type of visual information that is informative in the specific environment where the insect has to navigate in. The learning walks (that is, the movement) seem essential to assess what is informative. This is exploited by our simple pruning rule by looking at which PNs vary and which do not. How this rule can be implemented biologically remains

to be seen, but we can easily assume that KCs lose their connectivity to PNs that have no change in their firing activity [233, 26].

Visual worlds are different from olfactory worlds: impact on the MB connectivity

For maximizing the separation of inputs in the high dimensionality KC layer, combinatorics indicate that each KC should connect to half the PN population [127]. For our 162 PNs, this means there are 3.66×10^{47} connectivity patterns (see eq. (3)). This theoretical prediction may very well be useful in the case of olfaction, and actually was verified in the Locust olfactory system. However, we see here that this does not equally apply to visual information, as many KCs are similar to other KCs in their firing profiles along routes. This is because the visual world is strongly spatially structured and visual information varies drastically across the vertical axis of the eye regions in a way that is quite constant over multiple locations. Thus, if all olfactory receptors may have an equal chance of being useful, this is not the case with visual receptors given a navigational task. Our analysis shows that to avoid redundancy, KCs should connect in average to only 5-10% of PNs. Even if connecting to more PNs (towards 50% of PNs) would increase the likeliness that the connectivity pattern of each KCs is unique, this is not true regarding their input across a route. Note also that connecting to 5% of 162 PNs is already sufficient to produce 9.87×10^{12} different possible connectivity pattern (see eq. (3)) and is thus good enough to ensure, given the tens (or hundreds) of thousands of KCs present in ants, that the probability that two KCs would have the same connectivity pattern is extremely low.

We could thus draw as prediction that the Calyces of the Mushroom Bodies of visually navigating insects such as bees and ants should show less diverse connection profiles in the collar (visual) than in the lip (olfactory) of the Calyces. Continuous learning is not a problem, perhaps a solution Early models of visual navigation often encountered the problem of the number of views stored, and thus needed a mechanism to decide when to learn a view. This was a difficult task given that in natural environments, the view changes smoothly with displacement [344]. We show here that, by learning the view at every step of the agent (every 5 mm) and given the size of the virtual world (route across 60 m), our model essentially achieves continuous learning. This was also the case in the previous (albeit non based on the MB circuits) model of Baddeley et al. [10]. Over-sampling is not a problem here, given the fact that if the view is already familiar (e.g., it has been learnt 5 mm before) the same KCs will fire, and no change in connectivity in the KC-to-MBON synapses will happen. In other words, learning is only triggered by novelty. Despite such continuous learning, we can see that 10,000 KCs only are sufficient to memorise 60 m long route without memory saturation (fig. 3.6).

Potential improvements to the MB model

It is worth to note that we modelled here immediate learning (instant KC-to-MBON synaptic changes from 0.0 to 1.0), but the implementation of a smoother synaptic weight change would mean that only the KCs that fire in a stable way across several steps would contribute to learning. Thus, this should allow the model to learn more distal (and more useful) features quicker and filter out the proximal noise (e.g., small blades of grass that passes the retina quickly). However, the detection of the different motion patterns between proximal and distal features could also be done on the earlier stages of the visual pathways, as was for instance shown to be the case in lobula plate tangential cells in flies [147].

Also, we implemented here only one MBON for linear classification of the view familiarity, but insects Mushroom Bodies possess many output neurons conveying different valences [8, 111, 202, 208], allowing for instance for attractive and aversive responses pathways. The combination of such attractive and aversive visual memories can actually prove to be useful in navigation (chapter 4, [336]). However, our current conclusion about the impact of visual pre-processing should benefit to both attractive and repulsive pathways in the same way. There is evidence in bees of learning happening in the Calyces of the MBs, where a large octopaminergic neuron (VUM_{mx1}) encodes the innate response to sucrose and modulates the KC sensitivity to the PN inputs [95]. Thus, we can see how the potentiation of the PN-to-KC connection strength for important locations in the world would increase the chance to trigger these KCs, likely improving the signal to noise ratio for these particular locations.

Another element that would be worth implementing in our model is the existence of KC - KC excitatory connections [149], which could act as a temporal priming of the KC layer response between successive views [200]. This process could potentially account for the role of sequence learning in visual information, as for example observed in navigating ants [337, 252].

Finally, other types of PNs may be added to the model, for instance with PNs sampling large areas of the compound eye, such as the ones taking input in the Lobula [57, 205], could potentially convey higher-level image components extraction such as the detection of rotation-invariant features or image frequencies in the MB. It was indeed shown that some KCs in the drosophila Mushroom Body receive inputs from single PNs [63], these could carry such role. Such neurons may also be key to solve problems such as head pitch variation [4] which we did not tackle here.

Conclusion

Overall, this modelling work show the vital importance of visual pre-processing and appropriate connectivity to enable the Mushroom Body circuitry to memorise views and use these memories to output familiarity information. Given our simplification and conservative modelling, we show that lateral inhibition between neighbouring cartridge in addition to pruning of PN-KC connection at the onset of foraging, only 10,000 KCs can ensure continuous learning of more than 60-metres long routes in realistic virtual reconstruction of complex natural environment. Given the hundreds of thousands of KCs observed in the Mushroom Bodies of expert navigator such as ants and bees [174], as well as the myriads of additional processes that must actually happens in real brain (and that we did not model here), we can start to picture why these insects can navigate so robustly despite their tiny brain.

Chapter 4

Opponent processes in visual memories: A model of attraction and repulsion in navigating insects' mushroom bodies

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RESEARCH ARTICLE

Opponent processes in visual memories: A model of attraction and repulsion in navigating insects' mushroom bodies

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Abstract

Solitary foraging insects display stunning navigational behaviours in visually complex natural environments. Current literature assumes that these insects are mostly driven by attractive visual memories, which are learnt when the insect's gaze is precisely oriented toward the goal direction, typically along its familiar route or towards its nest. That way, an insect could return home by simply moving in the direction that appears most familiar. Here we show using virtual reconstructions of natural environments that this principle suffers from fundamental drawbacks, notably, a given view of the world does not provide information about whether the agent should turn or not to reach its goal. We propose a simple model where the agent continuously compares its current view with both goal and anti-goal visual memories, which are treated as attractive and repulsive respectively. We show that this strategy effectively results in an opponent process, albeit not at the perceptual level—such as those proposed for colour vision or polarisation detection—but at the level of the environmental space. This opponent process results in a signal that strongly correlates with the angular error of the current body orientation so that a single view of the world now suffices to indicate whether the agent should turn or not. By incorporating this principle into a simple agent navigating in reconstructed natural environments, we show that it overcomes the usual shortcomings and produces a step-increase in navigation effectiveness and robustness. Our findings provide a functional explanation to recent behavioural observations in ants and why and how so-called aversive and appetitive memories must be combined. We propose a likely neural implementation based on insects' mushroom bodies' circuitry that produces behavioural and neural predictions contrasting with previous models.

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Data Availability Statement: Code is available on GitHub (https://github.com/antnavigationteam/opponent_process_ploscompbio2020).

Author summary

Insects such as ants and bees are excellent navigators, able to learn long foraging routes and return to their nest in complex natural habitats. To achieve this, it is believed that individuals memorise views—the visual scene as they perceive it—only when their body is precisely oriented towards the goal. As a result, the insect can return to its goal by simply being attracted in the direction that represents the highest visual familiarity. Here we use a

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computational approach to show that this strategy suffers from a major weakness: a single view of the world does not suffice to tell whether the agent should turn or not to reach its goal. However, a surprisingly robust solution to this problem arises if we simply assume that these insects memorise not only goal-oriented views but also anti-goal-oriented views that they then treat as repulsive. This idea clarifies several observed behaviours that were difficult to explain with previous models. Overall, this research helps us to understand how insects combine memories in specific brain areas and can navigate so efficiently despite their tiny brain.

Introduction

Early naturalists were impressed by the navigational abilities of central place foragers such as bees, wasps and ants [1,2] and notably, from the comprehension that these abilities arose from a tiny volume of brain matter [3]. What mechanisms underlie insect navigation are still far from clear, however our understanding has considerably improved in the last decades. By combining experimental and computational approaches (e.g., [4]), this field has explored, tested and refined parsimonious hypotheses about insect navigational mechanisms [5]. Nowadays, advances in insect neurobiology [6,7] enable the design of biologically-realistic neural models to explore how such navigational mechanisms may be implemented in the insect brain [8–11]. The current work uses a computational approach to explore a novel hypothesis on the use and storage of visual memories for navigation. We chose to model an ants' perspective; however, we believe our conclusions can easily be extrapolated to other insect navigators.

Ant visual navigation and modelling

Naive ant foragers control their first journeys by relying heavily on Path Integration [12–14] or social cues [15,16]. These early-available solutions provide them with the opportunity to learn and memorise visual scenes for their subsequent journeys. They then predominantly rely upon these memories once experienced [17–19].

Modelling studies have proposed several types of algorithms to explain how insect memorise and use views for guidance. While most models assume that guidance is achieved by comparison of the currently perceived view to a memorised view (although this is still debated in bees [20,21]), they vary greatly on the way this is implemented (see [22] for a comprehensive classification). For instance, some homing models need to store only one view at the goal acting as an attractor [4,23] while others require multiple memorised views acting as direction setters pointing along a learnt route [18,24,25] or towards the goal [26–28]. Also, some models compare directly the raw visual input [29–32] while others are based on some specific visual processing such as distorting the current view [26], performing Fourier transformations [33,34], or extracting and recognising specific features from the environment [4].

Familiarity-based models

In the last decade, a particular type of models, which we call here 'familiarity-based' has gained attraction for it provides good explanations of a variety of observed ants' navigational behaviours [18,24,27,28], and is consistent with the insect's neural circuitry [9,29].

A key to these familiarity-based-models is that insects memorise visual scenes in an egocentric way, so that recognition is dependent on the insect's current head direction [35]. In other words, a current view will appear familiar only when the insect is aligned in (roughly) the

same direction than it was at the time of learning. If the insect is located at a familiar location, but its body is oriented in a wrong direction, its current view will appear unfamiliar. Perhaps counterintuitively, this direct coupling between visual familiarity and head direction can provide a solution for navigation. During learning, all one needs to do is to memorise views while facing a relevant direction, such as the direction of the nest as indicated by the Path Integrator [12,14]. The agent can therefore later seek the direction of the goal by simply looking for the most familiar direction of the current location. This strategy enables to recover a goal direction over tens of metres in complex outdoor environments [36,37] and, interestingly, is most robust when the scene is parsed at the low resolution of insect eyes [31,33].

This principle can be directly applied to recapitulate idiosyncratic routes, given a set of visual memories stored along them. Agent-based simulations have shown that the ‘walking forward in the most familiar direction’ rule enables agents to recapitulate routes [8,24,29,38] in a way that closely resembles what is observed in solitary foraging ants [18,39,40]. These models are further supported by the well-choreographed ‘learning walks’ displayed by ants—as well as the equivalent ‘learning flights’ displayed by bees and wasps [41–45]—around their nest (or a food source). During learning walks, ants appear to systematically pause while facing towards the nest (or a food source), presumably to memorise ‘correctly aligned’ views from multiple locations around the goal [12,14,46–48]. Given such a visual memory bank, models show that the exact same principle used for route following is able to produce a search centred on the goal location [24,27]. There again, the models’ emerging search patterns capture several aspects of the ants’ visually driven search [38,46,49,50].

The greatest appeal of familiarity-based models is that the comparison of the current and memorised view needs only to output one familiarity value. To get this familiarity value, there is no need for finding correspondence between parts of the visual field and a direction in the world. This contrasts with so called ‘correspondence models’ where features must be extracted from panoramas, and matched locally. Familiarity-based models do not need retinotopic mapping to be preserved at the comparison stage. This fits well the connectivity of the insect Mushroom Bodies [51], where memories of visual scenes are likely encoded [8,9]. Indeed, in visually navigating insects, the visual input as perceived through their low-resolution eyes and processed by early optic neural relays [52–54], is then projected to more than 100,000 Mushroom Body cells (Kenyon Cells: KCs) through an apparently random pattern of connections, likely disrupting retinotopic organisation [55–57]. Remarkably, given the synaptic plasticity observed at the output of the MB during learning [58–60], the resulting activity of the MB output neurons naturally provides a measure of familiarity of the current sensory input [8,51].

A simplified model of the ant and bees circuitry shows that the Mushroom Bodies provides enough ‘memory space’ for an agent to store the required visual information to recapitulate a 10 meter long-route in a naturalistic environment—here again, by simply following the rule of ‘walking forward in the most familiar direction’ [8].

Limits of familiarity-based models

Familiarity-based models have the advantage of capturing a wide range of observed behaviours (route following, nest search, the need for learning walks and scanning multiple directions when lost) while remaining remarkably simple and faithful to the known insect circuitry. However, they suffer from one main drawback: the familiarity of the view currently perceived does not tell whether the current direction is right or wrong. For instance, a view perceived when facing away from the nest can still provide a good match with a view acquired during learning walks (like when the insect was located on the other side of the nest), and thus appear highly familiar, although the current direction is dead wrong. Conversely, a view perceived

when facing towards the nest but several meters away from it may provide a rather poor match, although the current direction is correct. In other words, current familiarity does not correlate with directional error. Therefore, it is problematic for these models to infer a correct motor decision uniquely from the current visual familiarity.

Typically, familiarity-based models eschew this problem by using a ‘stop-scan-go’ strategy: at each step the agent stops and rotates on the spot to scan multiple directions; and subsequently moving in the direction that is most familiar for this particular location [8,24,26,27]. However, this procedure is (1) cumbersome, as it requires the agent to stop, rotate on the spot (i.e. to trigger a scan) and compute the familiarity for many directions at each step; (2) non-parsimonious, as it requires a three-stage process (i.e., scan/select a direction/step forward) and the assumption that the agent repeatedly stores and compares the familiarities across all sampled directions at each step, to select the highest one; (3) unrealistic, as ants and bees do not need to scan in order to home successfully.

A substitute to physically rotating on the spot could be to perform some sort of mental rotation [34]. However, it is yet difficult to see how mental rotation could be implemented in the insect brain. Such a feat would presumably require that visual encoding is achieved on the 360 visual field at once (as in [34]), but insects visual neuropils in each hemisphere seem to receive almost purely projections from the ipsilateral eyes, which visual field covers around 180 degrees only. Also, an ability for mental rotation seems hard to conciliate with the extensive physical scanning behaviours displayed by ants during a moment of visual uncertainty [61]. We decided here to remain entirely faithful to the known insect neural connectivity.

An alternative to performing rotations (either physically or mentally)–based on lateral oscillations–has been proposed for route following[25], but as we show here proves to be extremely sensitive to parameter change. This is expected as such an alternative does not solve the intrinsic problem that current familiarity does not correlate with directional error.

Our approach

We present here a simple and realistic solution the problem of previous familiarity-based models. We assumed that navigating insects store two separate memory banks in their Mushroom Bodies: one attractive–based on views learnt while facing the goal direction–and one repulsive–based on views learnt while facing the anti-goal direction, that is, 180° away from the goal direction; and that the output of both memory pathways are integrated downstream during navigation (Fig 1). These assumptions are sensible because they flow from behavioural and neurobiological observations rather than the desire to improve a model. First, ants of the genus *Myrmecia* were shown to display regular alternations between phases while facing the nest and when facing the opposite direction, suggesting that they may learn both attractive and repulsive visual memories [48]. Second, ants can associate views with an aversive valence, triggering turns when these views are subsequently experienced [62]. In insects’ brains, it is now clear that several output neurons from the Mushroom Bodies (so-called MBONs), which typically respond to learnt stimuli, convey either attraction or avoidance signals [58,63–65]; and that these MBON signals with opposite valences are integrated downstream [66–68].

We explored the effect of these assumptions using views taken from virtual reconstructions of ants’ natural outdoor environments [69]. Our results show that such an integration of visual memories is akin to an opponent process, and provides a qualitative gain in navigational information. Notably, the integrated signal now directly correlates with the angular error of the current direction and thus greatly facilitates the problem of steering. As a proof of concept, we implemented this opponent memory principle in a simplistic ant agent model [25]. This granted the agent the ability to home with much higher success, and drastically increased

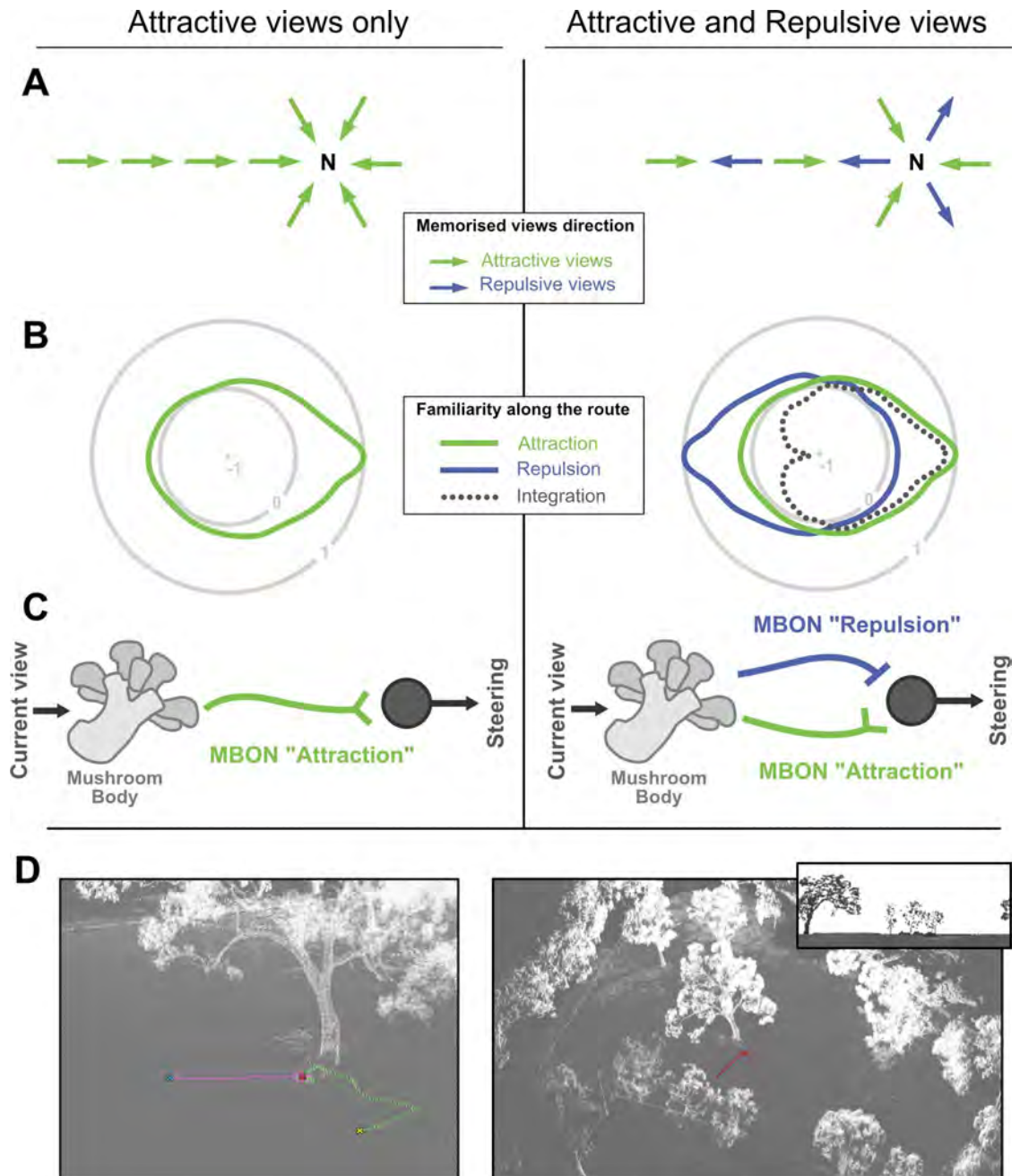


Fig 1. Model structure and core concept. A. Schematic representation of the spatial distribution of memorised views, assuming here the agent has learnt views around the nest and along a homing route. Left, only views with a positive valence (i.e. attractive) are learnt, all pointing towards the nest (N). Right, views with positive valence as well as views with negative valence (i.e. repulsive) are learnt. Repulsive views are directed 180° away from the nest. B. Schematic representation of the visual familiarity perceived across all 360° directions for a given position: here on the familiar route with the nest direction towards the right. Concentric circles represent the level of familiarity of the current view (i.e., how well it matches the memorised view) as a function of the direction of the current view: 0 indicates no match whereas 1 is a perfect match. Given the opponent integration of both memory pathway (dash line), negative values indicate directions for which the current view matches the repulsive memories better than the attractive ones. C. Scheme of the proposed neural implementation; the Mushroom Body receives information about the current view. Learning consist in modulating the connections elicited by goal oriented views with one Mushroom Body output neuron (MBON). When subsequent views are presented, the signal of the MBON thus correlate with the current visual familiarity (see [9] for more detail). With the opponent process (right), learning additionally involves anti-goal oriented views to be associated with another MBON conveying the opposite valence. Both MBONs are integrated downstream by simple subtraction before modulating the steering. D. Example snapshots of the virtual 3D worlds used in our navigation simulations. Coloured lines are paths of the agent. In inset, an example of what the model gets as visual input (horizontal resolution of 5°/pixel).

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robustness to both displacement and parameter changes. Our hypothesis makes clear behavioural and neurobiological predictions, as well as calls for further hypotheses which we discuss.

Results and discussion

The performance of insect visual navigators is typically thought to be based on visual memories acquired while facing in the correct goal direction [8,24–29,35,36,38,70–72]. This is strongly corroborated by the learning walks and learning flights of ants [12,14,46,47], bees [41,44,45] and wasps [42,43], where the individuals regularly turn back and look towards the goal direction, thus storing the information necessary to subsequently return to it. Indeed, with such a memory bank of goal-oriented views, the most familiar direction of each location tends to be directed along the route or towards the nest, resulting in ‘familiarity flows’ across space converging towards the goal (Fig 2A, left; as in [30–32,34]). Thus, all the insect needs to do to reach its goal is, at each location, to walk forward in the direction that presents the most familiar view [24,27,28].

The drawbacks of using only goal-oriented views

The problem of using only ‘goal-oriented’ visual memories becomes apparent when mapping the familiarity across multiple locations when always facing in a same direction (Fig 2B): with goal-oriented views only, familiarity increases as one gets closer to a location where a view facing in that same direction had been memorised (Fig 2B, left). As a result, the familiarity of a given view tends to correlate with distance from the nest but not with the angular difference from the nest direction (Fig 2C, left). That is to say, without scanning multiple orientations, familiarity does not reliably indicate whether one should turn or carry on straight ahead. For instance, we show that a view that is correctly oriented towards the goal can present the same familiarity as a view that is poorly oriented (180° opposite) from the goal (black and white squares in Fig 2B, left). To summarise, when using goal-oriented views only, one can infer the correct direction by scanning multiple directions at a given location (Fig 2A, left), but the familiarity of a given view, taken alone, is not informative about the current directional error and thus cannot be used directly for steering (Fig 2B, left).

Opponent processes in visual memories

We show here that the need for scanning can vanish entirely when assuming the co-existence of a second memory pathway, based on views learnt this time while facing in the anti-goal direction. This idea is corroborated by the recent observation that *Myrmecia* ants during their learning walks display oscillatory alternations between nest-facing and anti-nest-facing phases [48]. The key is that the familiarity signal outputted by the anti-goal memory pathway must be

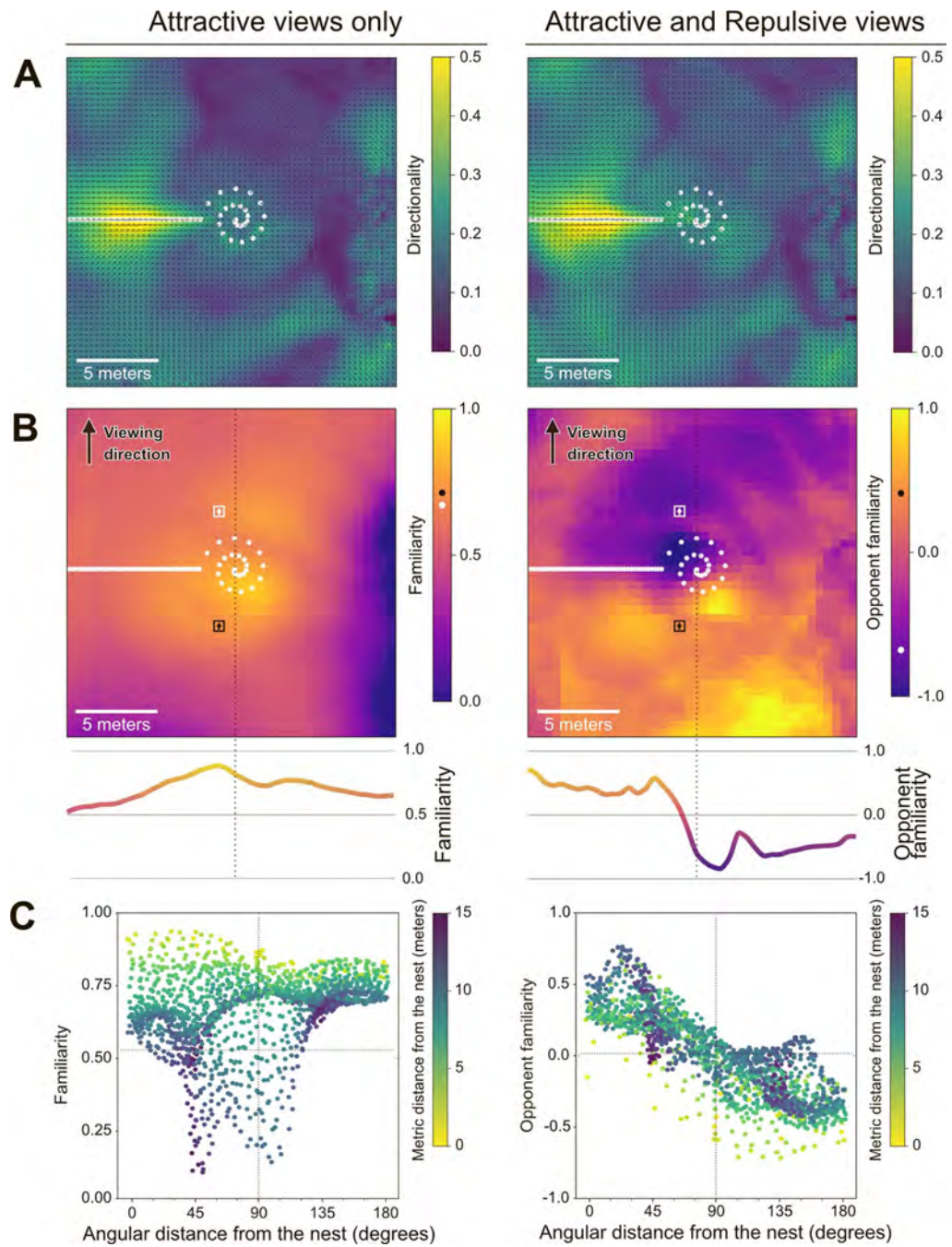


Fig 2. The statistics of opponent visual familiarity across space. A-C. Left column, Attractive views only; Right column, Attractive and Repulsive views. A. Top view spatial map of the directional specificity of the visual familiarity, on a 30 x 30 metres area centred on the nest given view stored around the nest and along a homing route (white dots). Arrows indicate the direction presenting the maximum familiarity for each position on the map. Colour and arrows lengths indicate the specificity of the best matching direction as compared to the other directions at this location (calculated as 'max familiarity'-'median familiarity'), normalised between 0.0 (least specific) and 0.5 (most specific). B. Visual familiarity across the same 30 x 30 area as in A, but given one facing direction only (North). Although this direction (North-facing) was picked rather arbitrarily, any other direction provided qualitatively similar results, with one exception: route-directed views. We deliberately excluded this direction, to show the apparent familiarity as seen from unfamiliar viewing directions. Familiarity values (colours) represent the match between the north facing view at this location and the memory bank (the view that gives the smallest difference), normalised between 1.0 (i.e., perfect match) and 0.0 (worst match). On the right panel, 'Opponent familiarity values' show the integration of both memory pathways, with negative values indicating that the view at this location matches better the repulsive memory bank. Two positions located on opposite sides of the nest (black and white squares) may appear similarly familiar (black and white dots on the colour map) given Attractive memory bank only (left panel) but show opposite valence given Attractive and Repulsive integration (right panel). The curves in the bottom panels, shows the familiarity along a transect passing through the nest (dash line). C. Scatter plot of the familiarity values of B, against the angular distance between the north facing view and the nest direction. Angular distance of 0° means that the north facing view is pointing towards the nest. Metric (Euclidean) distance of the position of the view from the nest is shown in the colour map.

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subtracted from the signal of the goal-oriented memory pathway (or the other way around). In other words, goal-oriented and anti-goal oriented memories pathways have opposite valence and can be considered as driving attraction and repulsion respectively. The signal resulting from this integration can be seen as determining whether the current view is attractive or repulsive.

This provides several benefits. First, at a given location, recovering the correct direction through scanning is facilitated because anti-goal memories tend to make anti-goal directions all the more repulsive, which thus increases the difference between incorrect and correct directions (Fig 1B, right). Second and most importantly, a single view is informative: across locations, views oriented towards the nest appear attractive, while views oriented away from the nest appear repulsive (Fig 1B, right). In other words, the 'opponent familiarity' resulting from such an integration is not correlated with distance from the goal but with the current directional error (Fig 1C, right) and can thus be used directly for steering (Fig 3).

The concept of integrating goal and anti-goal visual memory pathways is to some extent analogous to an opponent processes, albeit not at the perceptual level—such as what has been proposed for colour vision in primates [73] and bees [74] or polarisation vision in invertebrates [75–77]—but at the level of the environmental space. In the case of polarisation vision, R7/R8 polarisation-sensitive photoreceptors have orthogonal orientation: opponent polarisation neurons receive excitatory input by one direction of polarisation and inhibitory input from the orthogonal direction [75]. The key advantage of such process is that it provides consistency against variations of luminance levels. For instance, if the intensity of light decreases, both excitatory and inhibitory inputs decrease, but their ratio stays alike.

In much the same way, we propose here that 'opponent familiarity neurons' receive excitatory input from the familiarity signal based on the memories stored in one direction (e.g., goal oriented view) and inhibitory input from the familiarity signal based on memories stored in the opposite direction (e.g., anti-goal oriented view) (Fig 1C). The resulting signal provides consistency over overall variations in familiarity across locations. For instance, as one is getting closer to a familiar location, both inhibitory and excitatory familiarity pathways decrease but the sign of their difference stays alike. As a result, the opponent familiarity obtained is quite insensitive to variation in distance from the locations at which memories have been stored, but correlates remarkably well with the current directional error (Fig 2C, right). Obviously, in a completely unfamiliar environment, both memory pathways output similarly low familiarity values and the resulting opponent familiarity remains null whatever the direction currently faced.

Absolute mismatch values resulting from the comparison of two views are dependent on the structure of the scenes. Locations presenting rather homogenous visual patterns across

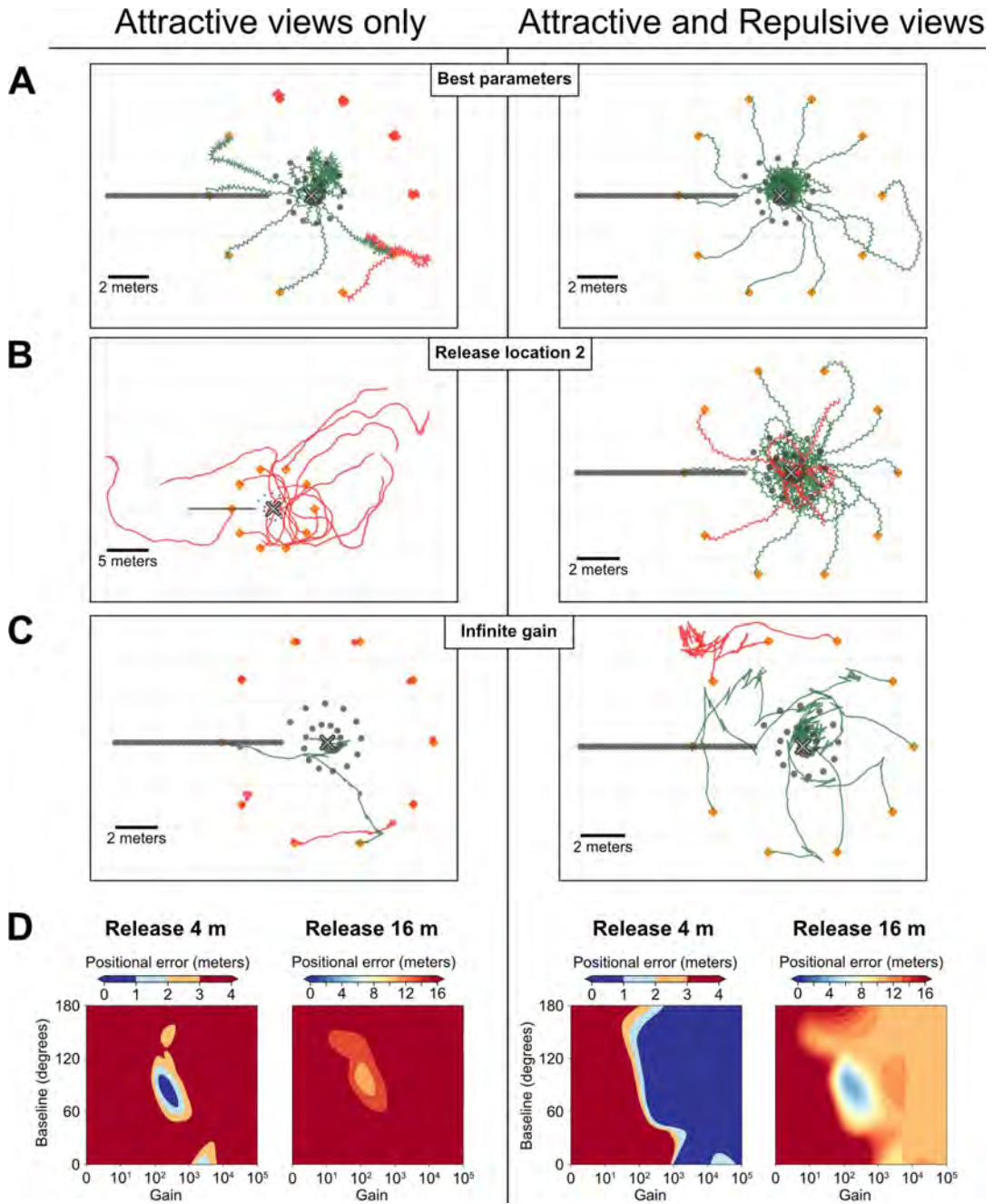


Fig 3. Efficiency in finding the nest of homing agents. A-D. Comparison of oscillatory agents implemented with attractive views only (left column) or using the opponent integration of attractive and repulsive views (right column). A-C. Example paths (120 steps) of 10 individual agents for each condition. Grey cross, nest; Grey dots, positions of the learnt views (facing towards the nest); Orange markers, release locations of the agents. Green paths correspond to agents that successfully ended up within 1-meter radius of the nest, red paths correspond to agents that failed to do so. A. Paths given the best set of parameters obtained for the 'Attractive-only agent' at this nest location. Note that as a result of the poor success of this model, agents staying at the starting point are favoured over agents straying further away. B. Paths of agent trained and tested at a second nest location in the virtual world, but using the parameter optimised for the location in A. Agents using Attractive view only appear less robust to changes in the environment. C. Example of a simulation with an infinite gain parameter, which constrains the model to 0° or 180° turns. Thanks to the addition of $\pm 20^\circ$ random noise on turning direction, the Attractive-Repulsive model can still home. D. Heatmaps representing homing success (median of 10 agents' arrival distance from the nest) across variations of two parameters. The 'baseline' indicates the turn angle effected in response to an average familiarity value (or when attractive familiarity = repulsive familiarity). The 'gain' is a value that convert the perceived familiarity into the turn modulation, which increases (if current attractive familiarity is low) or decreases (if current attractive familiarity is high) the turn amplitude in relation to the baseline. A high gain makes the agent very reactive to small change in familiarity. Agents using attractive view only requires a fine parameter tuning to home successfully at 4-meters, and no set of parameters allow for significant homing abilities from 16 metres or more. Agents released at 4m using the opponent integration of attractive and repulsive memories are robust as long as gain is above a threshold value, but parameter tuning can improve their performance from 16m.

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azimuths tend to yield low mismatches, while heterogonous scenes tend to yield high mismatches. For instance, if an agent ends up unusually close to a tree, the mismatch experienced may become unusually high, that is, the familiarity becomes unusually low (see for instance Fig 2B, left). Thus, what should be considered as a good or bad familiarity value is a tricky question, and this is why models using only attractive view without scanning are very sensitive to parameter calibration (Fig 3). This problem disappears when using an opponent process since the resulting 'opponent familiarity' is always relative to the two measurements: determining which of the two signals is stronger tells whether one is well oriented or not. In other words, instead of knowing 'how good is the current familiarity', the navigator assesses if 'the current view matches better with a good or a bad direction'. As a result, a glance in a single direction is sufficient to inform the decision to turn, or rather go forward.

Opponent visual memories enable robust navigation

To test whether such an opponent process in visual memories is actually helpful for navigation, we implemented it in a simple agent navigating in reconstructions of ants' natural environments (Fig 1D, S2 Fig). The goal of the following section is not to provide an exhaustive exploration of such a system, but to serve as a proof of concept that implementing two opponent memory banks in a navigating agent can be quite useful and straightforward. We chose a previously published simple agent that has the advantage to estimate the familiarity of a single view per step, rather than scanning multiple directions [25]. In this model, guidance involves an oscillator resulting in a continuous alternation between left and right turns, as observed in several insects, including ants [78–80]. The amplitude of the oscillations is simply modulated by the familiarity of the view currently perceived: familiar views trigger small turns, whereas unfamiliar views trigger large turns; however, the direction (left or right) of the turns is solely dependent on the current state of the oscillator. When using goal-facing memories only, this model can be sufficient for an agent to recapitulate a route in a natural-like environment [25]. This is because, as long as the agent stays on the familiar route, visual familiarity is higher when the currently faced direction is aligned with the correct route direction.

However, our parameters exploration shows that this 'attractive-views only' model is operational only given a small range of parameters (Fig 3D, left), and when operational, outputs mediocre homing performance (Fig 3A, left). Moreover, the range of parameters at which it operates in a given region of the world does not necessarily operates in other regions of the world (Fig 3B, left). Here again, this is because absolute mismatch values are strongly dependant on the visual structure of the scenes.

In contrast, when equipped with two memory banks acting as opponent processes, homing performance becomes much higher. Not only is the agent more accurate in searching at the goal location but homing becomes much more robust to variations in location (Fig 3A and 3B) and larger displacements, with successful homing from up to 16 metres in our Australian world given a learning walk spanning up to 2 meters around the nest (Fig 3D, S1 Fig). In other words, with the opponent process strategy, the agent is able to home robustly even when not inside a route corridor. Finally, and perhaps most importantly, homing becomes remarkably robust to changes in parameters (Fig 3D). Basically, it operates as long as the gain is above a given threshold value (Fig 3D). Briefly, 'gain' is a single-value parameter that converts a familiarity value into a turn amplitude, see Methods for details. A gain too small simply prevent the agent to execute sharp turns, and given that our agent is forced to step forward, it cannot reorient sharply enough to search at the goal. However, a gain too high seems to present no fundamental problem. An infinitely high gain makes the turn amplitude extremely sensitive to minute changes in familiarity perceived and thus constrains turn amplitude either to 180° (U-turn) when the view matches best the anti-nest memory bank or 0° (go straight ahead) when the view matches best the nest-oriented memory bank. Obviously in this binary condition (0° or 180° degree turn) the agent is doomed to be moving along straight line. However, providing a bit of random noise on the direction taken at each time step is sufficient to enable an agent with infinitely high gain to explore novel directions, and to eventually home successfully (Fig 3C).

The success of the agent is not due to the fact that it possesses twice as many memorised views than the previous agent with only nest-oriented memories. Given less than half the usual number of memorised views (10 of each, instead of 25 attractive-only), the agent using opponent process still homes well (Fig 4C). Furthermore, the position of nest and anti-nest oriented memories can be chosen quite arbitrarily (Fig 4A). Even though *Myrmecia crosslandi* ants appear to alternate regularly between nest and anti-nest facing directions [48], other species may not [61,81], and indeed according to our model, it is not needed. Also, as observed in ants, learning walks spanning larger areas provide larger catchment areas [82]. With our model, a learning walk spanning either a 0.5-metre radius or an 8-metre radius enables the agent to home reliably up to 8 and 16 metres respectively (S1 Fig), even though the number of memorised views remains the same. Interestingly, the agent still manages to pinpoint the goal given a learning walk spanning only a 10-centimetre radius if released in the vicinity (Fig 4E). Although, here the step length must be smaller than the usual 20 cm to ensure that the agent does not exit the small catchment area; after all, ants do tend to slow down when close to the goal [83]. Also, the model is readily able to navigate in a totally different virtual world such as the one reconstructed in the Spanish arid area of *Cataglyphis velox* ants [40] (Fig 4F), which presents much more local clutter and no distant landmarks (S2 Fig). Although here, because the views perceived change very rapidly with displacement, we needed to reduce the step length to prevent the agent to escape the familiar catchment area (Fig 4F).

Perhaps most interestingly, we observe that the memorised views need not be precisely oriented towards the goal or anti-goal direction. Homing is robust even to very large random deviations in memorised views orientation (e.g., $\pm 90^\circ$ around the goal and anti-goal directions) (Fig 4B). This may explain why ants displaying learning walks may not necessarily align their body precisely towards and away from the nest [12,48,61,81]. Finally, most of our simulations were achieved with a typical ant resolution of 5°/pixel [53], but resolution does not need to be precisely tuned either. For instance, we observe that the agent still homes well given a resolution of 10°/pixel (Fig 4D). Obviously, we expect that a too low or too high resolution would eventually disrupt the ability to home using such a visual matching strategy, as investigated elsewhere [31].

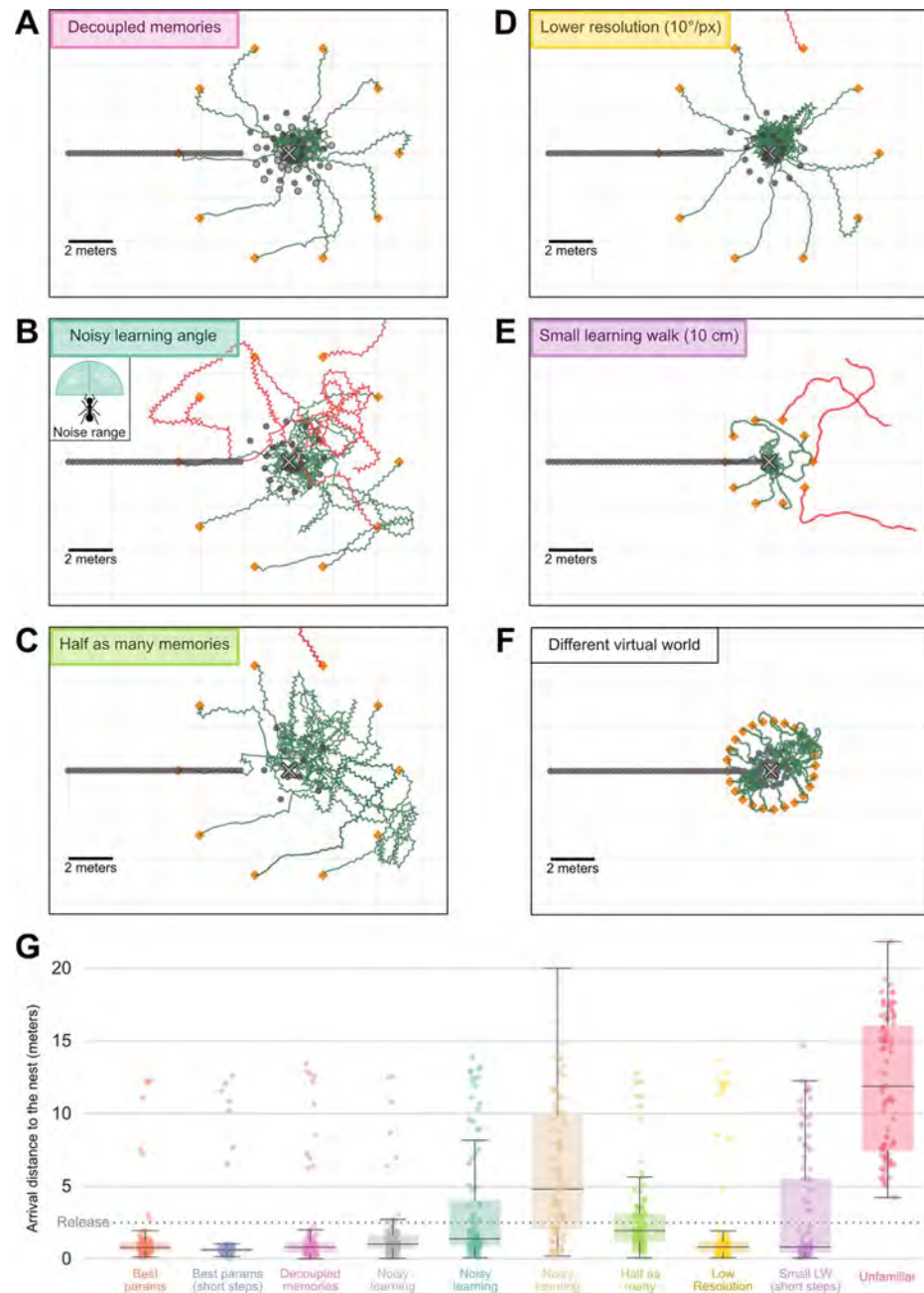


Fig 4. Robustness of agents using attractive and repulsive views. A-F. Paths (120 steps) of navigating agents using the opponent integration of attractive and repulsive views, in several experimental conditions. Symbols are the same as in Fig 3. A. Decoupled memories: attractive memories have been acquired at different locations (dark grey dots in a spiral) than the repulsive memories (light grey dots). B. Noisy learning angle: attractive and repulsive memories were acquired given a $\pm 90^\circ$ uniform noise in the viewing direction

around the goal and anti-goal direction. Inset, range of the noise. C. Half as many memories: only 10 learning walk views (instead of 25) were learnt. D. Smaller resolution: The visual input to the model is a coarser snapshot of the environment, with 10° /pixel (instead of 5° /pixel). E. Small learning walk: the learning walk along which memorised view are sampled span only a 10 centimetre radius around the nest (instead of 2 metres). The agent walked slower (4 times shorter steps, 4 times as many) in this condition. F. Test in a different virtual world, with more clutter and no distant landmarks (see S2 Fig). G. Boxplots of the arrival distance to the nest of agents released at 5m around the nest and walking for 30m (300 runs per conditions: 3 different nest locations in the virtual world x 100 release locations around each nest location). Conditions corresponds to the conditions mentioned above. 'Unfamiliar' corresponds to agents released around a fictive nest at an unfamiliar region in the virtual world.

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It is important to note that we did not wish here to explore thoroughly how this particular agent responds to these different variables. We rather wanted to show that the principle of an opponent process in visual memories provides robust information which can be directly exploited for successful navigation.

Neural implementation in the insect brain

The idea of using two memory pathways that interact antagonistically is directly inspired by insect neurobiology. Notably, recent work in *Drosophila melanogaster* has exposed the neural mechanisms underlying the formation and expression of aversive and appetitive memories in the Mushroom Bodies (MB) [63]. Stimuli identities are encoded as sparse activation patterns of specific Kenyon Cells (KCs). These KCs synapse onto multiple MB output neurons (MBONs), of which activities can, for example, favour an approach behaviour, or an avoidance behaviour [84,85]. Also, each MBON is associated with a dopaminergic neuron (DAN) conveying a specific reinforcement value. In a nutshell, during learning, the co-activation of a stimulus with a positive or negative reinforcer (DAN) decreases the stimulus elicited KCs' output synapses onto the associated appetitive or aversive MBONs respectively. Subsequently, this biases the stimulus-driven activity towards the residual pathway and thus favour either approach or avoidance behaviour [84,86].

Interestingly, these aversive and appetitive pathways are typically integrated in an antagonistic fashion, sometimes by having an 'aversive' MBON directly inhibiting a neighbour 'appetitive' MBON or by having MBONs with opposite valence conveying inhibitory and excitatory signals onto the same downstream neuron [63,66,67].

In fruit flies and honeybees, learning and memory involving the mushroom bodies is typically studied experimentally using olfactory stimuli [51,63,64,84,85,87–89]. Nonetheless, we observe abundant projections from visual areas to the MBs in visually navigating insects such as ants and bees [55,56,58,90,91] (and to a lesser extent, in *drosophila* [92]), and neural models show that the identity of visual scenes can be represented in specific KCs activities and enable route navigation [8,9].

Therefore, in simple terms, the current idea assumes that guidance in insect visual navigator is driven continuously from a balance between attraction and aversion. Goal-oriented views are learnt as appetitive while anti-goal-oriented views are learnt as aversive by having their respective KCs view-driven activity directed towards antagonistic MBONs (Fig 1C). Both MBON pathways are integrated and the resulting signal is used for triggering approach (i.e., inhibit turn) or avoidance (i.e. trigger turn). As we have shown, this simple scheme enables robust navigation.

Predictions and further hypotheses

The idea of using such opponent memory pathways for navigation yields predictions that contrast with previous models. Also, it enables us to formulate further hypotheses. We briefly state some of these below.

- Our model implies the activation of two different reinforcer signals to categorise whether views should be learnt as aversive or appetitive. One should be active while the ant is roughly facing in a specific direction (e.g., towards the goal), the other while the ant is facing in the opposite direction (e.g. away from the goal). One possibility is that these reinforcer neurons are under the control of the Path Integrator. This could be achieved by dopaminergic neurons conveying signals from the lateral accessory lobe (i.e. Central Complex output of path integration steering command) to the Mushroom Body lobes.
- Both appetitive and aversive pathway should convey antagonistic signals, which are likely implemented as inhibitory and excitatory synapses. The balance between attraction and aversion could thus be altered by pharmacologically by inoculating specific receptor antagonists (such as GABA receptor antagonist) in the output region of the MBONs.
- For ants at the exact nest location, visual familiarity should be very high for both opponent pathways, resulting in a balanced activity. In completely unfamiliar locations, familiarity is very low for both opponent pathways, resulting also in a balanced activity. This should be true for all directions at both of these locations. Therefore, the current model makes the counter-intuitive prediction that a similar behaviour is expected when the ant is located exactly at the nest and when in unfamiliar surroundings. We recently verified this prediction with ants tethered on an air suspended treadmill [93].
- Ants dragging a heavy food item backwards are aligned in the direction opposite to their direction of movement [94–96]. The existence of views with opposite valence learnt in the anti-goal direction may thus be recognised as repulsive and favour further backward motion when the ant body is facing away from the goal. Recent work seems to verify this prediction [97].
- Nest-oriented and anti-nest-oriented memories could be used to navigate along both inbound and outbound paths by swapping their respective valences. To achieve this, antagonist MBONs pathways could converge onto two different ‘opponent integrator neurons’ with opposite signs. Motivation for homing or foraging, which is believed to select a given memory bank [98–101], could instead select the ‘opponent integrator neuron’ with the correct sign. This could be tested behaviourally, by looking at whether homing ants released on its outbound route tend to be repulsed from the outbound direction.

Conclusion

We adapted the well-supported idea that insects continuously combine appetitive and aversive memory pathways [63] to the context of ant visual navigation by assuming that ants learn both attractive and repulsive views, when looking in opposite direction [48]. We showed that this effectively results in a process analogous to an opponent process, where the resulting signal is the relative difference between the two ‘directionally opponent’ visual familiarity measurements. Contrary to a single familiarity measurement, as usually assumed, this opponent signal correlates remarkably well with the current directional error and can be used directly to drive behaviour (without the need to scan) and produce robust navigation. Other models, such as ‘correspondence’ models [22], can also benefit from using both aversion and attraction components, this time across the visual field [4,72]. But these models have the limitation that retinotopy must be preserved in memory, which, contrary to familiarity-based model, does not fit the mushroom body connectivity. How such an opponent signal is actually processed to drive motor behaviour in various flying or walking insect navigators remains an open question but our model suggests that robust information for directional control is already present in the Mushroom Body output neural population.

Methods

This work aims at exposing the concept of how opponent-like processes in visual memories might be used for navigational tasks. To do so, we used a simple agent-based model in a closed loop with a 3D virtual environment. All following simulations were performed in Python 3.8.

Virtual world and acquisition of views

The virtual environment used in our model was generated by the software Habitat3D [102], an open-source tool which provides photorealistic meshes of natural scenes from point clouds acquired with help of a LiDAR scanner (IMAGER 5006i). This environment is mapped on the habitat of *Myrmecia* ants from Canberra, Australia [69]. The mesh spans a diameter of around 65 metres and features large eucalyptus trees and distant panorama cues. This dataset can be found on the Insect Vision webpage (<https://insectvision.dlr.de/3d-reconstruction-tools/habitat3d>). For speed optimization purposes, we down-sampled the originally high-resolution mesh with the open-source software Blender into a lower number of vertices; the rendering was then realized in OpenGL, with the Python libraries Plyfile and PyOpenGL.

This 3D model enabled us to render panoramic views from any location as a 360-degree picture. We chose input only to be the blue channel of the RGB scene, resulting in only one luminance value per pixel. Also, the skybox was made a pure blue uniform colour. That way, as with UV in natural scenes [103,104], blue provides a strong contrast between the sky and the terrestrial scene. This approximates the type of visual information used by navigating ants [105,106].

The rendered views were down-sampled to 72×27 px, (5°/pixel horizontal resolution) to roughly match the ant's eye resolution. Note that in one section we explored the effect of resolution (see "Parameters analysis"). Finally, these views were cropped vertically so that the bottom, floor-facing part was discarded. As a result, the visual information that the model receives is a small rectangular matrix of single-channel values representing the above-horizon panorama.

Memorised views and current familiarity

The agent is assumed to have stored a collection of memorised views around the nest and along a route (Fig 1A). During tests, the agent computes a value of visual familiarity at each time step by comparing its current view to its memory bank. This is achieved by calculating the global root mean square pixel difference [30] between the current view and each of the views in the memory bank and keeping the value of the lowest mismatch, as typically achieved in ant navigation studies [35,36,38,50,71,72,107], models [24,27,28,32,69] and inspired robotics [22,25,108]. This mismatch value provides an estimation of the unfamiliarity of the current view. We normalise unfamiliarity values to fit the range [0:1], and then subtract the obtained value to 1 in order to get what we thus call "familiarity". Note however that the views are not rotated but compared only according to the facing directions of the current and memorised views.

Combining attractive and repulsive visual memories

The novelty of this model is that the agent is assumed to have two independent memory banks: one 'attractive', and one 'repulsive'. The attractive memory bank includes 'learning walks views' memorised around the nest while pointing nest-ward, as well as 'homing route views' memorised along a straight, homebound route (Fig 1A). The repulsive memory bank

includes 'learning walks views' memorised around the nest while pointing out-ward (away from the nest), and possibly 'outbound route' views (see [Discussion](#)).

For simplicity, $N = 25$ learning walk views were assumed to be sampled along a 2m radius spiral around the nest and the homing route was chosen to be 10 metres long, fitting roughly with observed data in *Myrmecia* ants nesting in this environment [48]. We also ran simulations with other learning walk spans: 0.5, 2 and 8 metres (see [S1 Fig](#)).

At each time step, the agent computes two values of familiarity: one by comparing its current view to the attractive memory bank and one by comparing this same current view to the repulsive memory bank. These two familiarity values are assumed to have an antagonist effect on the ant's behaviour, their integration resulting in what we call here 'Opponent familiarity'. We modelled this by a simple subtraction:

$$\text{Opponent familiarity} = (\text{Attractive familiarity value} - \text{Repulsive familiarity value}) \quad \text{Eq 1}$$

This opponent familiarity is what constitutes our agent's overall drive, in the sense that it modulates the turning amplitude.

$$\text{Overall drive} = \text{Opponent familiarity} \quad \text{Eq 2}$$

For example, positive Opponent familiarity values (for 'attractive familiarity' > 'repulsive familiarity') cause the agent's current direction to be rather aligned with an attractive memorised view.

In situations where using only the attractive visual memories, the attractive familiarity value obtained was directly converted into the 'overall drive' (see below).

Using attractive views only

We tested the agent using the attractive memory bank only. In such cases, the Attractive familiarity value was used directly to generate the overall drive. To facilitate the comparison with the use of opponent visual memories (see previous section), we normalised the Attractive familiarity by subtracting an 'average world familiarity value' corresponding to the average familiarity obtained between two views in the world, estimated by comparing 32 views at random positions and orientation.

$$\text{Overall drive} = \text{Attractive familiarity value} - \text{average world familiarity value} \quad \text{Eq 3}$$

That way, the Overall drive is normalised around 0, as when combining Attractive and Repulsive memories. Positive values indicate a rather good match (high familiarity) while negative values indicate a rather poor match (low familiarity). Note that we performed a systematic parameter analysis that enabled us to pinpoint the best set of parameters (in that case, varying the 'baseline' parameter (see next section) amounted to varying this 'average familiarity value'). In other words, the rather arbitrary choice of the 'average world familiarity value' had no incidence on the following analysis.

Oscillatory agent

To drive the agent, we used a similar approach to the ones of Kodzhabashev and Mangan [25] and Wystrach et al., [80]. The agent is a simple dot in space (x, y) with a current heading (theta). The elevation of the agent (z) was fixed at a height of 2 centimetres above the ground. The agent has a continuously running oscillator alternating between left mode and right mode, which controls the instantaneous turning direction: the 'Turn direction' thus alternates at each time step (Left-Right-Left-Right-...) and is solely controlled by the oscillator. However, the 'Turn amplitude' is directly dependent on the current overall drive (see previous

section), that is, on the current visual familiarities.

$$\text{Turn amplitude (deg)} = \text{baseline} - (\text{gain} \times \text{overall drive}) \quad \text{Eq 4}$$

We used a single parameter (gain) to convert the overall drive into the angular value for the turn amplitude. The baseline was a fixed parameter which controlled the extent of the turn amplitude given an *Overall drive* = 0. Therefore, a positive overall drive will reduce the current turn amplitude from baseline towards 0 degrees (straight ahead), while a negative overall drive will increase the current turn amplitude from baseline towards 180 degrees (opposite direction). The turn amplitude was clipped between 0 and 180 degrees.

Across time steps (t), the agent's orientation (θ) will thus oscillate between left and right turns ($(-1)^t$). So, to update the current facing direction of the agent:

$$\theta_{(t+1)} = \theta_{(t)} + (\text{Turn amplitude} \times (-1)^t) + \text{noise} \quad \text{Eq 5}$$

At each time step, we added noise as a random angular value drawn from a Gaussian ($\mu = 0$; $\text{std} = 10 \text{ degrees}$). This was to ensure our model is robust to the intrinsic noise of the real world.

Once released at a given location, the agent repeats the current rules at each time step:

1. Obtain the current view and compute its corresponding overall drive (Eqs 1 and 2 or Eq 3)
2. Turn on the spot (turn amplitude determined by Eq 4, turn direction determined by the oscillator state: Eq 5)
3. Walk 1 step forward (we set 1 step = 20 cm)

It is useful to note that the turn performed in rule 2 represents the direction in which the forward step will be performed, and not a turn performed independently from the forward motion as in 'stop and scan' models.

We released the agent equipped with its Attractive and Repulsive memory banks (or Attractive only memory bank) at different release points, and let it run in a closed loop with the environment, and observed the resulting paths (Figs 3 and 4).

Sampling of the apparent familiarity

To analyse the differences between direct (Attractive only) and opponent (Attractive–Repulsive) memories, we performed a somewhat exhaustive sampling of the apparent visual familiarity around the nest: we defined a lattice of 3600 sampling positions, covering a square region of 30×30 metres centred on the nest, every 50 cm. On each of these positions, an agent was positioned and acquired a reading of the visual familiarity in all the directions (72 positions all around, i.e. every 5 degrees). We thus obtained maps of the familiarity in this area, for both memory types (Fig 2).

Parameter analysis

We performed a systematic parameter analysis to determine the range of gain and baseline in which the agent is able to operate. For each combination of parameters, M individual runs of 320 steps (enabling the agent to walk $320 \times 0.2 = 64$ meters) were performed from M different release points, equally spaced around the nest ($M = 10$, i.e. one every 36 degrees around the nest). For each of these individual runs, the initial walking direction was randomly picked. The following parameters were varied:

1. Release distance: The release distance was varied between 0 and 32 metres away from the nest, which correspond to the limits of our reconstructed world. Most agents were unable to home when released at 32 metres.
2. Learning walk span: we ran parameter exploration simulations with three different learning walk spans: 0.5, 2 and 8 metres (S1 Fig).
3. Oscillator baseline: As described in the ‘Oscillating agent’ section, the oscillator driving the turning direction has a baseline firing value. We varied this baseline between 0 degrees (= no spontaneous oscillations, the agent can only up-regulate the turn amplitude when the view is rather repulsive) and 180 degrees (= spontaneous full U-turn, the agent can only down-regulate turn amplitude when the view is rather attractive).
4. Gain: The turning amplitude is governed by the gain as described in the ‘Oscillating agent’ section. We varied this gain parameter between 0 and +inf.

The success of each parameter combination was determined by taking the median arrival distance (i.e., distance from the nest after the 320 steps) of the 10 individual agents. We chose the median as it provides a good estimation as to whether the majority of agents could reach the nest, while the mean would be very sensitive to the paths effected by lost agents.

Finally, we also investigated the robustness of using opponent process memories by adding the following constraints:

- Directional noise during learning: the angle at which the learning walk views were taken was submitted to angular noise (up to 90 degrees in both directions, randomly taken from a uniform distribution)
- Attractive/Repulsive memories decoupling: the positions at which Attractive and Repulsive view were taken were made uncorrelated, by using two different learning walk spirals.

Supporting information

S1 Fig. Effect of the learning walk span. Heatmaps of the interaction between the gain and baseline parameters, and their effect on homing success (distance of arrival at the end of the simulation), for two sizes of learning walks and three release distances.
(TIFF)

S2 Fig. Virtual 3D worlds. Snapshots of the 3D point clouds of the two virtual environments used in this work. Top, Canberra environment, large scale and large distant features such as trees; Bottom, Sevilla environment, with high clutter and no distal panorama.
(TIFF)

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References

1. Wehner R. Early ant trajectories: spatial behaviour before behaviourism. *Journal Of Comparative Physiology A, Neuroethology, Sensory, Neural, And Behavioral Physiology*. 2016; 202: 247–266. <https://doi.org/10.1007/s00359-015-1060-1> PMID: 26898725
2. Fabre JHC. Souvenirs entomologiques: études sur l'instinct et les moeurs des insectes. C. Delagrave; 1890.
3. Darwin C. On the Manner of Development of Man from Some Lower Form. *Descent of Man*. D. Appleton; 1896.
4. Cartwright BA, Collett TS. Landmark learning in bees—experiments and models. *Journal of Comparative Physiology*. 1983; 151: 521–543.
5. Wystrach A, Graham P. What can we learn from studies of insect navigation? *Animal Behaviour*. 2012; 84: 13–20. <https://doi.org/10.1016/j.anbehav.2012.04.017>
6. Seelig JD, Jayaraman V. Neural dynamics for landmark orientation and angular path integration. *Nature*. 2015; 521: 186–191. <https://doi.org/10.1038/nature14446> PMID: 25971509
7. Honkanen A, Adden A, Freitas J da S, Heinze S. The insect central complex and the neural basis of navigational strategies. *Journal of Experimental Biology*. 2019; 222: jeb188854. <https://doi.org/10.1242/jeb.188854> PMID: 30728235
8. Ardin P, Peng F, Mangan M, Lagogiannis K, Webb B. Using an Insect Mushroom Body Circuit to Encode Route Memory in Complex Natural Environments. *PLoS Computational Biology*. 2016; 12: e1004683. <https://doi.org/10.1371/journal.pcbi.1004683> PMID: 26866692
9. Webb B, Wystrach A. Neural mechanisms of insect navigation. *Current Opinion in Insect Science*. 2016; 15: 27–39. <https://doi.org/10.1016/j.cois.2016.02.011> PMID: 27436729
10. Stone T, Webb B, Adden A, Weddig NB, Honkanen A, Templin R, et al. An Anatomically Constrained Model for Path Integration in the Bee Brain. *Current Biology*. 2017; 27: 3069–3085.e11. <https://doi.org/10.1016/j.cub.2017.08.052> PMID: 28988858
11. Le Moëll F, Stone T, Lihoreau M, Wystrach A, Webb B. The Central Complex as a Potential Substrate for Vector Based Navigation. *Front Psychol*. 2019; 10. <https://doi.org/10.3389/fpsyg.2019.00690> PMID: 31024377
12. Müller M, Wehner R. Path Integration Provides a Scaffold for Landmark Learning in Desert Ants. *Current Biology*. 2010; 20: 1368–1371. <https://doi.org/10.1016/j.cub.2010.06.035> PMID: 20619653
13. Schwarz S, Wystrach A, Cheng K. Ants' navigation in an unfamiliar environment is influenced by their experience of a familiar route. *Scientific reports*. 2017; 7: 14161. <https://doi.org/10.1038/s41598-017-14036-1> PMID: 29074991
14. Fleischmann PN, Christian M, Müller VL, Rössler W, Wehner R. Ontogeny of learning walks and the acquisition of landmark information in desert ants, *Cataglyphis fortis*. *Journal of Experimental Biology*. 2016; jeb–140459.
15. Collett TS, Graham P, Durier V. Route learning by insects. *Current Opinion in Neurobiology*. 2003; 13: 718–725. <https://doi.org/10.1016/j.conb.2003.10.004> PMID: 14662374
16. Czaczkes TJ, Grüter C, Ratnieks FLW. Trail Pheromones: An Integrative View of Their Role in Social Insect Colony Organization. *Annual Review of Entomology*. 2015; 60: 581–599. <https://doi.org/10.1146/annurev-ento-010814-020627> PMID: 25386724
17. Wehner R, Räber F. Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia*. 1979; 35: 1569±1571.

18. Wystrach A, Schwarz S, Schultheiss P, Beugnon G, Cheng K. Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology*. 2011; 197: 167–179. <https://doi.org/10.1007/s00359-010-0597-2> PMID: 20972570
19. Collett M, Chittka L, Collett TS. Spatial memory in insect navigation. *Current biology: CB*. 2013; 23: R789–R800. <https://doi.org/10.1016/j.cub.2013.07.020> PMID: 24028962
20. Cheeseman JF, Millar CD, Greggers U, Lehmann K, Pawley MD, Gallistel CR, et al. Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *Proceedings of the National Academy of Sciences*. 2014; 111: 8949–8954.
21. Cheung A, Collett M, Collett TS, Dewar A, Dyer F, Graham P, et al. Still no convincing evidence for cognitive map use by honeybees. *Proceedings of the National Academy of Sciences*. 2014; 111: E4396–E4397.
22. Möller R, Vardy A. Local visual homing by matched-filter descent in image distances. *Biological Cybernetics*. 2006; 95: 413–430. <https://doi.org/10.1007/s00422-006-0095-3> PMID: 17021827
23. Mangan M, Webb B. Modelling place memory in crickets. *Biological Cybernetics*. 2009; 101: 307–323. <https://doi.org/10.1007/s00422-009-0338-1> PMID: 19862550
24. Baddeley B, Graham P, Husbands P, Philippides A. A model of ant route navigation driven by scene familiarity. *PLoS Comput Biol*. 2012; 8: e1002336. <https://doi.org/10.1371/journal.pcbi.1002336> PMID: 22241975
25. Kodzhabashev A, Mangan M. *Route Following Without Scanning*. Biomimetic and Biohybrid Systems. Springer; 2015. pp. 199–210.
26. Ralf Möller. A model of ant navigation based on visual prediction. *Journal of Theoretical Biology*. 2012; 305: Pages 118–130. <https://doi.org/10.1016/j.jtbi.2012.04.022> PMID: 22554981
27. Wystrach A, Mangan M, Philippides A, Graham P. Snapshots in ants? New interpretations of paradigmatic experiments. *The Journal of Experimental Biology*. 2013; 216: 1766–1770. <https://doi.org/10.1242/jeb.082941> PMID: 23348949
28. Graham P, Philippides A, Baddeley B. Animal cognition: multi-modal interactions in ant learning. *Current Biology*. 2010; 20: R639–R640. <https://doi.org/10.1016/j.cub.2010.06.018> PMID: 20692612
29. Ardin P, Mangan M, Wystrach A, Webb B. How variation in head pitch could affect image matching algorithms for ant navigation. *Journal of Comparative Physiology A*. 2015; 201: 585–597.
30. Zeil J, Hofmann MI, Chahl JS. Catchment areas of panoramic snapshots in outdoor scenes. *Journal of the Optical Society of America a-Optics Image Science and Vision*. 2003; 20: 450–469.
31. Wystrach A, Dewar A, Philippides A, Graham P. How do field of view and resolution affect the information content of panoramic scenes for visual navigation? A computational investigation. *Journal of Comparative Physiology A*. 2016; 202: 87–95.
32. Dewar AD, Philippides A, Graham P. What is the relationship between visual environment and the form of ant learning-walks? An in silico investigation of insect navigation. *Adaptive Behavior*. 2014; 22: 163–179.
33. Stürzl W, Mallot HA. Efficient visual homing based on Fourier transformed panoramic images. *Robotics and Autonomous Systems*. 2006; 54: 300–313. <https://doi.org/10.1016/j.robot.2005.12.001>
34. Thomas Stone, Michael Mangan, Antoine Wystrach, Barbara Webb. Rotation invariant visual processing for spatial memory in insects. *Interface Focus*. 2018; 8: 20180010. <https://doi.org/10.1098/rsfs.2018.0010> PMID: 29951190
35. Zeil J. Visual homing: an insect perspective. *Current Opinion in Neurobiology*. 2012; 22: 285–293. <https://doi.org/10.1016/j.conb.2011.12.008> PMID: 22221863
36. Narendra A, Gourmaud S, Zeil J. Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. *Proceedings of the Royal Society B: Biological Sciences*. 2013; 280. <https://doi.org/10.1098/rspb.2013.0683> PMID: 23804615
37. Philippides A, Baddeley B, Cheng K, Graham P. How might ants use panoramic views for route navigation? *Journal of Experimental Biology*. 2011; 214: 445–451. <https://doi.org/10.1242/jeb.046755> PMID: 21228203
38. Wystrach A, Cheng K, Sosa S, Beugnon G. Geometry, features, and panoramic views: Ants in rectangular arenas. *Journal of Experimental Psychology: Animal Behavior Processes*. 2011; 37: 420–435. <https://doi.org/10.1037/a0023886> PMID: 21604907
39. Kohler M, Wehner R. Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors? *Neurobiology of Learning and Memory*. 2005; 83: 1–12. <https://doi.org/10.1016/j.nlm.2004.05.011> PMID: 15607683

40. Mangan M, Webb B. Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*). *Behavioral Ecology*. 2012; 23: 944–954.
41. Philippides A, de Ibarra NH, Riabinina O, Collett TS. Bumblebee calligraphy: the design and control of flight motifs in the learning and return flights of *Bombus terrestris*. *The Journal of Experimental Biology*. 2013; 216: 1093–1104. <https://doi.org/10.1242/jeb.081455> PMID: 23447668
42. Zeil J. Orientation flights of solitary wasps (*Cerceris*, Sphecidae, Hymenoptera) .1. Description of flight. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology*. 1993; 172: 189–205.
43. Stürzl W, Zeil J, Boeddeker N, Hemmi JM. How Wasps Acquire and Use Views for Homing. *Current Biology*. 2016; 26: 470–482. <https://doi.org/10.1016/j.cub.2015.12.052> PMID: 26877083
44. Couvillon PA, Leiato TG, Bitterman ME. Learning by honeybees (*Apis mellifera*) on arrival at and departure from a feeding place. *Journal of Comparative Psychology*. 1991; 105: 177. <https://doi.org/10.1037/0735-7036.105.2.177> PMID: 1860311
45. Lehrer M. Bees which turn back and look. *Naturwissenschaften*. 1991; 78: 274–276.
46. Judd SPD, Collett TS. Multiple stored views and landmark guidance in ants. *Nature*. 1998; 392: 710–714.
47. Nicholson DJ, Judd SPD, Cartwright BA, Collett TS. Learning walks and landmark guidance in wood ants (*Formica rufa*). *Journal of Experimental Biology*. 1999; 202: 1831–1838. PMID: 10359685
48. Jayatilaka P, Murray T, Narendra A, Zeil J. The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*. *Journal of Experimental Biology*. 2018; 221: jeb185306. <https://doi.org/10.1242/jeb.185306> PMID: 30127076
49. Wehner R, Michel B, Antonsen P. Visual navigation in insects: Coupling of egocentric and geocentric information. *Journal of Experimental Biology*. 1996; 199: 129–140. PMID: 9317483
50. Schultheiss P, Wystrach A, Legge ELG, Cheng K. Information content of visual scenes influences systematic search of desert ants. *The Journal of Experimental Biology*. 2012. <https://doi.org/10.1242/jeb.075077> PMID: 23125338
51. Heisenberg M. Mushroom body memoir: from maps to models. *Nat Rev Neurosci*. 2003; 4: 266–275. <https://doi.org/10.1038/nrn1074> PMID: 12671643
52. Gronenberg W. Structure and function of ant (Hymenoptera: Formicidae) brains: strength in numbers. *Myrmecological News*. 2008; 11: 25–36.
53. Schwarz S, Narendra A, Zeil J. The properties of the visual system in the Australian desert ant *Melophorus bagoti*. *Arthropod Structure & Development*. 2011; 40: 128–134.
54. Zollikofer CPE, Wehner R, Fukushi T. Optical Scaling in Conspecific *Cataglyphis* Ants. *Journal of Experimental Biology*. 1995; 198: 1637–1646. PMID: 9319542
55. Paulk AC, Gronenberg W. Higher order visual input to the mushroom bodies in the bee, *Bombus impatiens*. *Arthropod structure & development*. 2008; 37: 443–458.
56. Gronenberg W, López-Riquelme GO. Multisensory convergence in the mushroom bodies of ants and bees. *Acta Biologica Hungarica*. 2004; 55: 31–37. <https://doi.org/10.1556/ABiol.55.2004.1-4.5> PMID: 15270216
57. Gronenberg W. Subdivisions of hymenopteran mushroom body calyces by their afferent supply. *Journal of Comparative Neurology*. 2001; 435: 474–489. <https://doi.org/10.1002/cne.1045> PMID: 11406827
58. Strube-Bloss Martin F., Rössler Wolfgang. Multimodal integration and stimulus categorization in putative mushroom body output neurons of the honeybee. *Royal Society Open Science*. 5: 171785. <https://doi.org/10.1098/rsos.171785> PMID: 29515886
59. Cohn R, Morante I, Ruta V. Coordinated and Compartmentalized Neuromodulation Shapes Sensory Processing in *Drosophila*. *Cell*. 2015; 163: 1742–1755. <https://doi.org/10.1016/j.cell.2015.11.019> PMID: 26687359
60. Cassenaer S, Laurent G. Conditional modulation of spike-timing-dependent plasticity for olfactory learning. *Nature*. 2012; 482: 47. <https://doi.org/10.1038/nature10776> PMID: 22278062
61. Wystrach A, Philippides A, Aurejac A, Cheng K, Graham P. Visual scanning behaviours and their role in the navigation of the Australian desert ant *Melophorus bagoti*. *Journal of Comparative Physiology A*. 2014; 1–12.
62. Wystrach A, Buehlmann C, Schwarz S, Cheng K, Graham P. Avoiding pitfalls: Trace conditioning and rapid aversive learning during route navigation in desert ants. *bioRxiv*. 2019; 771204. <https://doi.org/10.1101/771204>

63. Cognigni P, Felsenberg J, Waddell S. Do the right thing: neural network mechanisms of memory formation, expression and update in *Drosophila*. *Current Opinion in Neurobiology*. 2018; 49: 51–58. <https://doi.org/10.1016/j.conb.2017.12.002> PMID: 29258011
64. Jarriault D, Fuller J, Hyland BI, Mercer AR. Dopamine release in mushroom bodies of the honey bee (*Apis mellifera* L.) in response to aversive stimulation. *Scientific Reports*. 2018; 8: 16277. <https://doi.org/10.1038/s41598-018-34460-1> PMID: 30389979
65. Schleyer M, Fendt M, Schuller S, Gerber B. Associative learning of stimuli paired and unpaired with reinforcement: Evaluating evidence from maggots, flies, bees and rats. *Frontiers in psychology*. 2018; 9: 1494. <https://doi.org/10.3389/fpsyg.2018.01494> PMID: 30197613
66. Aso Y, Hattori D, Yu Y, Johnston RM, Iyer NA, Ngo T-T, et al. The neuronal architecture of the mushroom body provides a logic for associative learning. *Elife*. 2014; 3: e04577. <https://doi.org/10.7554/eLife.04577> PMID: 25535793
67. Felsenberg J, Jacob PF, Walker T, Barnstedt O, Edmondson-Stait AJ, Pleijzier MW, et al. Integration of parallel opposing memories underlies memory extinction. *Cell*. 2018; 175: 709–722. <https://doi.org/10.1016/j.cell.2018.08.021> PMID: 30245010
68. Eichler K, Li F, Litwin-Kumar A, Park Y, Andrade I, Schneider-Mizell CM, et al. The complete connectome of a learning and memory centre in an insect brain. *Nature*. 2017; 548: 175–182. <https://doi.org/10.1038/nature23455> PMID: 28796202
69. Stürzl W, Griaix I, Mair E, Narendra A, Zeil J. Three-dimensional models of natural environments and the mapping of navigational information. *Journal of Comparative Physiology A*. 2015; 201: 563–584.
70. Collett M. How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences of the United States of America*. 2010; 107: 11638–11643. <https://doi.org/10.1073/pnas.1001401107> PMID: 20534539
71. Wystrach A, Beugnon G, Cheng K. Landmarks or panoramas: what do navigating ants attend to for guidance? *Frontiers in Zoology*. 2011; 8: 21. <https://doi.org/10.1186/1742-9994-8-21> PMID: 21871114
72. Wystrach A, Beugnon G, Cheng K. Ants might use different view-matching strategies on and off the route. *The Journal of Experimental Biology*. 2012; 215: 44–55. <https://doi.org/10.1242/jeb.059584> PMID: 22162852
73. Hurvich LM, Jameson D. An opponent-process theory of color vision. *Psychological review*. 1957; 64: 384. <https://doi.org/10.1037/h0041403> PMID: 13505974
74. Backhaus W. Color opponent coding in the visual system of the honeybee. *Vision research*. 1991; 31: 1381–1397. [https://doi.org/10.1016/0042-6989\(91\)90059-e](https://doi.org/10.1016/0042-6989(91)90059-e) PMID: 1891826
75. Labhart T. How polarization-sensitive interneurons of crickets perform at low degrees of polarization. *Journal of experimental biology*. 1996; 199: 1467–1475. PMID: 9319364
76. Marshall J, Cronin TW. Polarisation vision. *Current Biology*. 2011; 21: R101–R105. <https://doi.org/10.1016/j.cub.2010.12.012> PMID: 21300269
77. Wehner R. The polarization vision project, championing organismic biology. In: Schildberger K, Elsner N, editors. *Neural Basis of Behavioural Adaptations*. Stuttgart, New York: G. Fischer; 1994. pp. 103–143.
78. Namiki S, Kanzaki R. The neurobiological basis of orientation in insects: insights from the silkmoth mating dance. *Current Opinion in Insect Science*. 2016; 15: 16–26. <https://doi.org/10.1016/j.cois.2016.02.009> PMID: 27436728
79. Lent DD, Graham P, Collett TS. Phase-Dependent Visual Control of the Zigzag Paths of Navigating Wood Ants. *Current Biology*. 2013; 23: 2393–2399. <https://doi.org/10.1016/j.cub.2013.10.014> PMID: 24268412
80. Wystrach A, Lagogiannis K, Webb B. Continuous lateral oscillations as a core mechanism for taxis in *Drosophila* larvae. *Elife*. 2016; 5: e15504. <https://doi.org/10.7554/eLife.15504> PMID: 27751233
81. Fleischmann PN, Grob R, Wehner R, Rössler W. Species-specific differences in the fine structure of learning walk elements in *Cataglyphis* ants. *Journal of Experimental Biology*. 2017; 220: 2426–2435. <https://doi.org/10.1242/jeb.158147> PMID: 28679795
82. Fleischmann PN, Rössler W, Wehner R. Early foraging life: spatial and temporal aspects of landmark learning in the ant *Cataglyphis noda*. *J Comp Physiol A*. 2018; 204: 579–592. <https://doi.org/10.1007/s00359-018-1260-6> PMID: 29679143
83. Buehlmann C, Fernandes ASD, Graham P. The interaction of path integration and terrestrial visual cues in navigating desert ants: what can we learn from path characteristics? *Journal of Experimental Biology*. 2018; 221: jeb167304. <https://doi.org/10.1242/jeb.167304> PMID: 29146769
84. Oswald D, Felsenberg J, Talbot CB, Das G, Perisse E, Huetteroth W, et al. Activity of Defined Mushroom Body Output Neurons Underlies Learned Olfactory Behavior in *Drosophila*. *Neuron*. 2015; 86: 417–427. <https://doi.org/10.1016/j.neuron.2015.03.025> PMID: 25864636

85. Perisse E, Oswald D, Barnstedt O, Talbot CB, Huetteroth W, Waddell S. Aversive learning and appetitive motivation toggle feed-forward inhibition in the *Drosophila* mushroom body. *Neuron*. 2016; 90: 1086–1099. <https://doi.org/10.1016/j.neuron.2016.04.034> PMID: 27210550
86. Aso Y, Sitaraman D, Ichinose T, Kaun KR, Vogt K, Belliard-Guérin G, et al. Mushroom body output neurons encode valence and guide memory-based action selection in *Drosophila*. *eLife*. 2014;3. <https://doi.org/10.7554/eLife.04580> PMID: 25535794
87. Haenicke J, Yamagata N, Zwaka H, Nawrot M, Menzel R. Neural Correlates of Odor Learning in the Presynaptic Microglomerular Circuitry in the Honeybee Mushroom Body Calyx. *eNeuro*. 2018; 5. <https://doi.org/10.1523/ENEURO.0128-18.2018> PMID: 29938214
88. Devaud J-M, Papouin T, Carcaud J, Sandoz J-C, Grünewald B, Giurfa M. Neural substrate for higher-order learning in an insect: Mushroom bodies are necessary for configural discriminations. *PNAS*. 2015; 112: E5854–E5862. <https://doi.org/10.1073/pnas.1508422112> PMID: 26460021
89. Schleyer M, Saumweber T, Nahrendorf W, Fischer B, von Alpen D, Pauls D, et al. A behavior-based circuit model of how outcome expectations organize learned behavior in larval *Drosophila*. *Learning & Memory*. 2011; 18: 639–653.
90. Gronenberg W, Holldobler B. Morphologic representation of visual and antennal information in the ant brain. *Journal of Comparative Neurology*. 1999; 412: 229–240. [https://doi.org/10.1002/\(sici\)1096-9861\(19990920\)412:2<229::aid-cne4>3.0.co;2-e](https://doi.org/10.1002/(sici)1096-9861(19990920)412:2<229::aid-cne4>3.0.co;2-e) PMID: 10441753
91. Ehmer B, Gronenberg W. Segregation of visual input to the mushroom bodies in the honeybee (*Apis mellifera*). *Journal of Comparative Neurology*. 2002; 451: 362–373. <https://doi.org/10.1002/cne.10355> PMID: 12210130
92. Vogt K, Aso Y, Hige T, Knapek S, Ichinose T, Friedrich AB, et al. Direct neural pathways convey distinct visual information to *Drosophila* mushroom bodies. *Elife*. 2016; 5: e14009. <https://doi.org/10.7554/eLife.14009> PMID: 27083044
93. Murray T, Kocsi Z, Dahmen H, Narendra A, Le Möel F, Wystrach A, et al. The role of attractive and repellent scene memories in ant homing (*Myrmecia croelandi*). *Journal of Experimental Biology*. 2019.
94. Schwarz S, Mangan M, Zeil J, Webb B, Wystrach A. How Ants Use Vision When Homing Backward. *Current Biology*. 2017; 27: 401–407. <https://doi.org/10.1016/j.cub.2016.12.019> PMID: 28111152
95. Pfeffer SE, Wittlinger M. How to find home backwards? Navigation during rearward homing of *Cataglyphis fortis* desert ants. *Journal of Experimental Biology*. 2016; 219: 2119–2126. <https://doi.org/10.1242/jeb.137786> PMID: 27445399
96. Ardin PB, Mangan M, Webb B. Ant homing ability is not diminished when traveling backwards. *Frontiers in behavioral neuroscience*. 2016; 10: 69. <https://doi.org/10.3389/fnbeh.2016.00069> PMID: 27147991
97. Schwarz S, Clement L, Gkaniats E, Wystrach A. How do backward walking ants (*Cataglyphis velox*) cope with navigational uncertainty? *bioRxiv*. 2019.
98. Wehner R, Boyer M, Loertscher F, Sommer S, Menzi U. Ant navigation: One-way routes rather than maps. *Current Biology*. 2006; 16: 75–79. <https://doi.org/10.1016/j.cub.2005.11.035> PMID: 16401425
99. Harris RA, Hempel de Ibarra NH, Graham P, Collett TS. Ant navigation—Priming of visual route memories. *Nature*. 2005; 438: 302–302. <https://doi.org/10.1038/438302a> PMID: 16292300
100. Cruse H, Wehner R. No need for a cognitive map: decentralized memory for insect navigation. *Plos Computational Biology*. 2011; 7. <https://doi.org/10.1371/journal.pcbi.1002009> PMID: 21445233
101. Hoinville T, Wehner R, Cruse H. Learning and retrieval of memory elements in a navigation task. *Conference on Biomimetic and Biohybrid Systems*. Springer; 2012. pp. 120–131.
102. Risse B, Mangan M, Stürzl W, Webb B. Software to convert terrestrial LiDAR scans of natural environments into photorealistic meshes. *Environmental modelling & software*. 2018; 99: 88–100.
103. Differt D, Möller R. Insect models of illumination-invariant skyline extraction from UV and green channels. *Journal of theoretical biology*. 2015; 380: 444–462. <https://doi.org/10.1016/j.jtbi.2015.06.020> PMID: 26113191
104. Stone T, Mangan M, Ardin P, Webb B. Sky segmentation with ultraviolet images can be used for navigation. *Robotics: Science and Systems*. *Robotics: Science and Systems*; 2014.
105. Schultheiss P, Wystrach A, Schwarz S, Tack A, Delor J, Nooten SS, et al. Crucial role of ultraviolet light for desert ants in determining direction from the terrestrial panorama. *Animal Behaviour*. 2016; 115: 19–28.
106. Graham P, Cheng K. Ants use the panoramic skyline as a visual cue during navigation. *Current Biology*. 2009; 19: R935–R937. <https://doi.org/10.1016/j.cub.2009.08.015> PMID: 19889365

107. Freas CA, Wystrach A, Narendra A, Cheng K. The view from the trees: nocturnal bull ants, *Myrmecia midas*, use the surrounding panorama while descending from trees. *Frontiers in psychology*. 2018; 9: 16. <https://doi.org/10.3389/fpsyg.2018.00016> PMID: 29422880
108. Knight JC, Sakhapov D, Domcsek N, Dewar AD, Graham P, Nowotny T, et al. Insect-Inspired Visual Navigation On-Board an Autonomous Robot: Real-World Routes Encoded in a Single Layer Network. The 2018 Conference on Artificial Life: A Hybrid of the European Conference on Artificial Life (ECAL) and the International Conference on the Synthesis and Simulation of Living Systems (ALIFE). MIT Press; 2019. pp. 60–67.

Chapter 5

Towards a multi-level understanding in insect navigation

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Towards a multi-level understanding in insect navigation

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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.

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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^{**},6,7], 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 Ref. [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 properties 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 behavior – 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

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.

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 neuroimaging 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 complicates 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

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 subcomponents. 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.

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

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.

predictions can then be tested by respectively recording and stimulating neurons of navigating animals (Box 4).

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.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Jonas E, Kording K: **Could a neuroscientist understand a microprocessor?** *PLoS Comput Biol* 2017, **13**:e1005268 <http://dx.doi.org/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. Gomez-Marin A, Ghazanfar AA: **The life of behavior.** *Neuron* •• 2019, **104**:25–36 <http://dx.doi.org/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. Krakauer JW, Ghazanfar AA, Gomez-Marin A, MacIver MA, Poeppl D: **Neuroscience needs behavior: correcting a reductionist bias.** *Neuron* 2017, **93**:480–490 <http://dx.doi.org/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. Marr D: *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information.* New York, NY: Henry Holt and Co, Inc.; 1982. vol. 2, no. 4.2.
5. Wehner R: **Early ant trajectories: spatial behaviour before behaviourism.** *J Comp Physiol A* 2016, **202**:247–266 <http://dx.doi.org/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. Menzel R: **A short history of studies on intelligence and brain in honeybees.** *Apidologie* 2020 <http://dx.doi.org/10.1007/s13592-020-00794-x>.
7. Wystrach A, Graham P: **What can we learn from studies of insect navigation?** *Anim Behav* 2012, **84**:13–20 <http://dx.doi.org/10.1016/j.anbehav.2012.04.017>.
8. Heinze S, Narendra A, Cheung A: **Principles of insect path integration.** *Curr Biol* 2018, **28**:R1043–R1058 <http://dx.doi.org/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. Honkanen A, Adden A, da Silva Freitas J, Heinze S: **The insect central complex and the neural basis of navigational strategies.** *J Exp Biol* 2019, **222**(Suppl. 1):jeb188854 <http://dx.doi.org/10.1242/jeb.188854>. Recent and very complete review of the insect navigational behaviours that are based on path integration and compass representation.
10. Webb B: **Can robots make good models of biological behaviour?** *Behav Brain Sci* 2001, **24**:1033–1050 <http://dx.doi.org/10.1017/S0140525X01000127>.

11. Beer RD: **6 - The dynamics of brain-body-environment systems: a status report.** In *Handbook of Cognitive Science*. Edited by Calvo, Gomila A. San Diego: Elsevier; 2008:99-120.
12. Clark A: *Being There: Putting Brain, Body, and World Together Again*. MIT Press; 1998.
13. von Uexküll J: *Umwelt und Innenwelt der Tiere*. Berlin, Heidelberg: Springer Berlin Heidelberg; 1921.
14. Collett TS: **Path integration: how details of the honeybee waggle dance and the foraging strategies of desert ants might help in understanding its mechanisms.** *J Exp Biol* 2019, **222** <http://dx.doi.org/10.1242/jeb.205187>.
15. Graham P, Philippides A: **Vision for navigation: what can we learn from ants?** *Arthropod Struct Dev* 2017, **46**:718-722 <http://dx.doi.org/10.1016/j.asd.2017.07.001>.
16. Buehlmann C, Graham P, Hansson BS, Knaden M: **Desert ants use olfactory scenes for navigation.** *Anim Behav* 2015, **106**:99-105 <http://dx.doi.org/10.1016/j.anbehav.2015.04.029>.
17. Wolf H, Wehner R: **Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*.** *J Exp Biol* 2000, **203**:857-868 <http://dx.doi.org/10.5167/uzh-636>.
18. Baba Y, Tsukada A, Comer CM: **Collision avoidance by running insects: antennal guidance in cockroaches.** *J Exp Biol* 2010, **213**:2294-2302 <http://dx.doi.org/10.1242/jeb.036996>.
19. Buatois A, Lihoreau M: **Evidence of trapline foraging in honeybees.** *J Exp Biol* 2016, **219**:2426-2429 <http://dx.doi.org/10.1242/jeb.143214>.
20. Wystrach A, Buehlmann C, Schwarz S, Cheng K, Graham P: **Rapid aversive and memory trace learning during route navigation in desert ants.** *Curr Biol* 2020 <http://dx.doi.org/10.1016/j.cub.2020.02.082>. S096098222030289X.
21. Collett TS, Fry SN, Wehner R: **Sequence learning by honeybees.** *J Comp Physiol A* 1993, **172** <http://dx.doi.org/10.1007/BF00195395>.
22. Macquart D, Latil G, Beugnon G: **Sensorimotor sequence learning in the ant *Gigantiops destructor*.** *Anim Behav* 2008, **75**:1693-1701 <http://dx.doi.org/10.1016/j.anbehav.2007.10.023>.
23. Collett M, Graham P, Collett TS: **Insect navigation: what backward walking reveals about the control of movement.** *Curr Biol* 2017, **27**:R141-R144 <http://dx.doi.org/10.1016/j.cub.2016.12.037>.
24. Schwarz S, Clement L, Gkaniias E, Wystrach A: **How do backward walking ants (*Cataglyphis velox*) cope with navigational uncertainty?** *Anim Behav Cogn* 2019 <http://dx.doi.org/10.1101/2019.12.16.877704>. preprint.
25. Kohler M, Wehner R: **Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path-integration vectors?** *Neurobiol Learn Mem* 2005, **83**:1-12 <http://dx.doi.org/10.1016/j.nlm.2004.05.011>.
26. Mangan M, Webb B: **Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*).** *Behav Ecol* 2012, **23**:944-954 <http://dx.doi.org/10.1093/beheco/ars051>.
27. Collett M, Chittka L, Collett TS: **Spatial memory in insect navigation.** *Curr Biol* 2013, **23**:R789-800 <http://dx.doi.org/10.1016/j.cub.2013.07.020>.
28. Cartwright BA, Collett TS: **Landmark learning in bees: experiments and models.** *J Comp Physiol* 1983, **151**:521-543 <http://dx.doi.org/10.1007/BF00605469>.
29. Wehner R, Rüber F: **Visual spatial memory in desert ants, *Cataglyphis bicoior* (Hymenoptera: Formicidae).** *Experientia* 1979, **35**:1569-1571 <http://dx.doi.org/10.1007/BF01953197>.
30. Zeil J, Hofmann MI, Chahl JS: **Catchment areas of panoramic snapshots in outdoor scenes.** *J Opt Soc Am A* 2003, **20**:450 <http://dx.doi.org/10.1364/JOSAA.20.000450>.
31. Graham P, Cheng K: **Ants use the panoramic skyline as a visual cue during navigation.** *Curr Biol* 2009, **19**:R935-R937 <http://dx.doi.org/10.1016/j.cub.2009.08.015>.
32. Wehner R, Müller M: **Piloting in desert ants: pinpointing the goal by discrete landmarks.** *J Exp Biol* 2010, **213**:4174-4179 <http://dx.doi.org/10.1242/jeb.050674>.
33. Wystrach A, Cheng K, Sosa S, Beugnon G: **Geometry, features, and panoramic views: ants in rectangular arenas.** *J Exp Psychol: Anim Behav Processes* 2011, **37**:420-435 <http://dx.doi.org/10.1037/a0023886>.
34. Wystrach A, Beugnon G, Cheng K: **Landmarks or panoramas: what do navigating ants attend to for guidance?** *Front Zool* 2011, **8**:21 <http://dx.doi.org/10.1186/1742-9994-8-21>.
35. Collett TS, Lent DD, Graham P: **Scene perception and the visual control of travel direction in navigating wood ants.** *Philos Trans R Soc B: Biol Sci* 2014, **369** <http://dx.doi.org/10.1098/rstb.2013.0035>.
36. Lent DD, Graham P, Collett TS: **Phase-dependent visual control of the zigzag paths of navigating wood ants.** *Curr Biol* 2013, **23**:2393-2399 <http://dx.doi.org/10.1016/j.cub.2013.10.014>.
37. Wystrach A, Philippides A, Aurejac A, Cheng K, Graham P: **Visual scanning behaviours and their role in the navigation of the Australian desert ant *Melophorus bagoti*.** *J Comp Physiol A* 2014, **200**:615-626 <http://dx.doi.org/10.1007/s00359-014-0900-8>.
38. Baddeley B, Graham P, Husbands P, Philippides A: **A model of ant route navigation driven by scene familiarity.** *PLoS Comput Biol* 2012, **8** <http://dx.doi.org/10.1371/JOURNAL.PCBI.1002336> e1002336.
39. Fleischmann PN, Grob R, Wehner R, Rössler W: **Species-specific differences in the fine structure of learning walk elements in *Cataglyphis* ants.** *J Exp Biol* 2017, **220**:2426-2435 <http://dx.doi.org/10.1242/jeb.158147>.
40. Jayatilaka, Murray T, Narendra A, Zeil J: **The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*.** *J Exp Biol* 2018, **221** <http://dx.doi.org/10.1242/JEB.185306> jeb185306.
41. Müller M, Wehner R: **Path integration provides a scaffold for landmark learning in desert ants.** *Curr Biol* 2010, **20**:1368-1371 <http://dx.doi.org/10.1016/j.cub.2010.06.035>.
42. Philippides A, de Ibarra NH, Riabina O, Collett TS: **Bumblebee calligraphy: the design and control of flight motifs in the learning and return flights of *Bombus terrestris*.** *J Exp Biol* 2013, **216**:1093-1104 <http://dx.doi.org/10.1242/jeb.081455>.
43. Stürzl W, Zeil J, Boeddeker N, Hemmi JM: **How Wasps acquire and use views for homing.** *Curr Biol* 2016, **26**:470-482 <http://dx.doi.org/10.1016/j.cub.2015.12.052>.
44. Zeil J, Kelber A, Voss R: **Structure and function of learning flights in ground-nesting bees and wasps.** *J Exp Biol* 1996, **199**:245-252.
45. Kuenen LS, Baker TC: **A non-anemotactic mechanism used in pheromone source location by flying moths.** *Physiol Entomol* 1983, **8**:277-289 <http://dx.doi.org/10.1111/j.1365-3032.1983.tb00360.x>.
46. Namiki S, Kanzaki R: **The neurobiological basis of orientation in insects: insights from the silkworm mating dance.** *Curr Opin Insect Sci* 2016, **15**:16-26 <http://dx.doi.org/10.1016/j.cois.2016.02.009>.
47. Wystrach A, Lagogiannis K, Webb B: **Continuous lateral oscillations as a core mechanism for taxis in *Drosophila* larvae.** *eLife* 2016, **5**:e15504 <http://dx.doi.org/10.7554/eLife.15504>.
48. Kodzhabashev A, Mangan M: **Route following without scanning.** In *Biomimetic and Biohybrid Systems*, vol 9222. Edited by Wilson S, Verschure FMJ, Mura A, Prescott TJ. Cham: Springer International Publishing; 2015:199-210.
49. Le Moël F, Wystrach A: **Opponent processes in visual memories: a model of attraction and repulsion in navigating insects mushroom bodies.** *PLoS Comput Biol* 2020, **16**:e1007631 <http://dx.doi.org/10.1371/journal.pcbi.1007631>.
50. Murray T et al.: **The role of attractive and repellent scene memories in ant homing (*Myrmecia croslandi*).** *J Exp Biol* 2020, **223** <http://dx.doi.org/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. Webb B: **The internal maps of insects.** *J Exp Biol* 2019, **222**(Pt • Suppl. 1) <http://dx.doi.org/10.1242/jeb.188094> 06.
A review of insect navigational strategies that revolves around the computation level, with good insights about the place of modelling.
52. Heisenberg M: **Mushroom body memoir: from maps to models.** *Nat Rev Neurosci* 2003, **4**:266-275 <http://dx.doi.org/10.1038/nrn1074>.
53. Smith D, Wessnitzer J, Webb B: **A model of associative learning in the mushroom body.** *Biol Cybern* 2008, **99**:89-103 <http://dx.doi.org/10.1007/s00422-008-0241-1>.
54. Ardin, Peng F, Mangan M, Lagogiannis K, Webb B: **Using an insect mushroom body circuit to encode route memory in complex natural environments.** *PLoS Comput Biol* 2016, **12** <http://dx.doi.org/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. Webb B, Wystrach A: **Neural mechanisms of insect navigation.** *Curr Opin Insect Sci* 2016, **15**:27-39 <http://dx.doi.org/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. Kamhi JF, Barron AB, Narendra A: **Vertical lobes of the mushroom bodies are essential for view-based navigation in Australian *Myrmecia* ants.** *Curr Biol* 2020, **30**:3432-3437.e3 <http://dx.doi.org/10.1016/j.cub.2020.06.030>.
57. Buehlmann C, Wozniak B, Goulard R, Webb B, Graham P, Niven JE: **Mushroom bodies are required for learned visual navigation, but not for innate visual behavior, in ants.** *Curr Biol* 2020, **30**:3438-3443.e2 <http://dx.doi.org/10.1016/j.cub.2020.07.013>.
58. Cheung A: **Animal path integration: a model of positional uncertainty along tortuous paths.** *J Theor Biol* 2014, **341**:17-33 <http://dx.doi.org/10.1016/j.jtbi.2013.09.031>.
59. Dacke M, el Jundi B: **The dung beetle compass.** *Curr Biol* 2018, **28**:R993-R997 <http://dx.doi.org/10.1016/j.cub.2018.04.052>.
60. Dacke M *et al.*: **Multimodal cue integration in the dung beetle compass.** *Proc Natl Acad Sci U S A* 2019, **116**:14248-14253 <http://dx.doi.org/10.1073/pnas.1904308116>.
61. Müller M, Wehner R: **Wind and sky as compass cues in desert ant navigation.** *Naturwissenschaften* 2007, **94**:589-594 <http://dx.doi.org/10.1007/s00114-007-0232-4>.
62. Wystrach A, Schwarz S, Schultheiss, Baniel A, Cheng K: **Multiple sources of celestial compass information in the Central Australian desert ant *Melophorus bagoti*.** *J Comp Physiol A* 2014, **200**:591-601 <http://dx.doi.org/10.1007/s00359-014-0899-x>.
63. Wystrach A, Schwarz S: **Ants use a predictive mechanism to compensate for passive displacements by wind.** *Curr Biol* 2013, **23**:R1083-R1085 <http://dx.doi.org/10.1016/j.cub.2013.10.072>.
64. Pfeiffer K, Homberg U: **Organization and functional roles of the central complex in the insect brain.** *Annu Rev Entomol* 2014, **59**:165-184 <http://dx.doi.org/10.1146/annurev-ento-011613-162031>.
65. Seelig JD, Jayaraman V: **Neural dynamics for landmark orientation and angular path integration.** *Nature* 2015, **521**:186-191 <http://dx.doi.org/10.1038/nature14446>.
66. Sun X, Mangan M, Yue S: **An analysis of a ring attractor model for cue integration.** In *Biomimetic and Biohybrid Systems*, vol 10928. Edited by Vouloutsis V, Halloy J, Mura A, Mangan M, Lepora N, Prescott TJ, Verschure PFMJ. Cham: Springer International Publishing; 2018:459-470.
67. Touretzky DS: **Attractor network models of head direction cells.** *Head Direction Cells and the Neural Mechanisms of Spatial Orientation*. 2005:411-432.
68. W.E. Skaggs, J.J. Knierim, H.S. Kudrimoti, B.L. McNaughton, A Model of the Neural Basis of the Rats Sense of Direction, p. 10.
69. Song, Wang X-J: **Angular path integration by moving "Hill of Activity": a spiking neuron model without recurrent excitation of the head-direction system.** *J Neurosci* 2005, **25**:1002-1014 <http://dx.doi.org/10.1523/JNEUROSCI.4172-04.2005>.
70. Fiore VG, Kottler B, Gu X, Hirth F: **In silico interrogation of insect central complex suggests computational roles for the ellipsoid body in spatial navigation.** *Front Behav Neurosci* 2017, **11** <http://dx.doi.org/10.3389/fnbeh.2017.00142>.
71. Green J, Adachi A, Shah KK, Hirokawa JD, Magani S, Maimon G: **A neural circuit architecture for angular integration in *Drosophila*.** *Nature* 2017, **546**:101-106 <http://dx.doi.org/10.1038/NATURE22343>.
72. Kakaria KS, de Bivort BL: **Ring attractor dynamics emerge from a spiking model of the entire protocerebral bridge.** *Front Behav Neurosci* 2017, **11** <http://dx.doi.org/10.3389/fnbeh.2017.00008>.
73. Kim SS, Rouault H, Druckmann S, Jayaraman V: **Ring attractor dynamics in the *Drosophila* central brain.** *Science* 2017, **356**:849-853 <http://dx.doi.org/10.1126/science.aal4835>.
74. Su T-S, Lee W-J, Huang Y-C, Wang C-T, Lo C-C: **Coupled symmetric and asymmetric circuits underlying spatial orientation in fruit flies.** *Nat Commun* 2017, **8**:139 <http://dx.doi.org/10.1038/s41467-017-00191-6>.
75. Turner-Evans D *et al.*: **Angular velocity integration in a fly heading circuit.** *eLife* 2017, **6**:e23496 <http://dx.doi.org/10.7554/eLife.23496>.
76. Collins LT: **The case for emulating insect brains using anatomical "wiring diagrams" equipped with biophysical models of neuronal activity.** *Biol Cybern* 2019, **113**:465-474 <http://dx.doi.org/10.1007/s00422-019-00810-z>.
77. Stone T *et al.*: **An anatomically constrained model for path integration in the bee brain.** *Curr Biol* 2017, **27**:3069-3085.e11 <http://dx.doi.org/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. Pfeffer SE, Wittlinger M: **How to find home backwards? Navigation during rearward homing of *Cataglyphis fortis* desert ants.** *J Exp Biol* 2016, **219**:2119-2126 <http://dx.doi.org/10.1242/jeb.137786>.
79. Riley J *et al.*: **Compensation for wind drift by bumble-bees.** *Nature* 1999, **400**:126 <http://dx.doi.org/10.1038/22029>.
80. Pisokas I, Heinze S, Webb B: **The head direction circuit of two insect species.** *Neuroscience* 2019 . preprint, Accessed: Dec. 10, 2019. [Online]. Available: <http://biorxiv.org/lookup/doi/10.1101/854521>.
81. Wystrach A: **Insect spatial learning, a stroll through Tinbergens four questions.** *Encyclopedia of animal behavior*, 2019 2019.
82. Rosenblueth A, Wiener N: **The role of models in science.** *Philos Sci* 1945, **12**:316-321 <http://dx.doi.org/10.1086/286874>.
83. Cueva CJ, Wang Y, Chin M, Wei X-X: **Emergence of functional and structural properties of the head direction system by optimization of recurrent neural networks.** *arXiv:1912.10189 [cs, q-bio, stat]* 2019 . Accessed: Jan. 03, 2020. [Online]. Available: <http://arxiv.org/abs/1912.10189>.
84. Banino A *et al.*: **Vector-based navigation using grid-like representations in artificial agents.** *Nature* 2018, **557**:7705 <http://dx.doi.org/10.1038/s41586-018-0102-6>.
85. Collett M: **How navigational guidance systems are combined in a desert ant.** *Curr Biol* 2012, **22**:927-932 <http://dx.doi.org/10.1016/j.cub.2012.03.049>.
86. Legge EL, Wystrach A, Spetch ML, Cheng K: **Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted**

- integration of celestial and terrestrial cues. *J Exp Biol* 2014, **217**:4159-4166 <http://dx.doi.org/10.1242/jeb.107862>.**
87. Bregy, Sommer S, Wehner R: **Nest-mark orientation versus vector navigation in desert ants.** *J Exp Biol* 2008, **211**:1868-1873 <http://dx.doi.org/10.1242/jeb.018036>.
88. Wystrach A, Mangan M, Webb B: **Optimal cue integration in ants.** *Proc R Soc B: Biol Sci* 2015, **282** <http://dx.doi.org/10.1098/rspb.2015.1484> 20151484.
89. Wehner R: *The architecture of the desert ants navigational toolkit (Hymenoptera: Formicidae)*. . p. 12 2009.
90. Buehlmann C, Mangan M, Graham P: **Multimodal interactions in insect navigation.** *Anim Cogn* 2020 <http://dx.doi.org/10.1007/s10071-020-01383-2>.
91. Cruse H, Wehner R: **No need for a cognitive map: decentralized memory for insect navigation.** *PLoS Comput Biol* 2011, **7** <http://dx.doi.org/10.1371/journal.pcbi.1002009> e1002009.
92. Hoinville T, Wehner R, Cruse H: **Learning and retrieval of memory elements in a navigation task.** *Biomimetic and Biohybrid Systems*. 2012:120-131 http://dx.doi.org/10.1007/978-3-642-31525-1_11. Berlin, Heidelberg.
93. Wehner R, Hoinville T, Cruse H, Cheng K: **Steering intermediate courses: desert ants combine information from various navigational routines.** *J Comp Physiol A* 2016, **202**:459-472 <http://dx.doi.org/10.1007/s00359-016-1094-z>.
94. Hoinville T, Wehner R: **Optimal multiguideance integration in insect navigation.** *Proc Natl Acad Sci U S A* 2018, **115**:2824-2829 <http://dx.doi.org/10.1073/pnas.1721668115>.
95. Sun X, Yue S, Mangan M: **A decentralised neural model explaining optimal integration of navigational strategies in insects.** *bioRxiv* 2020 <http://dx.doi.org/10.1101/856153>. 856153.

Discussion

This thesis presented a computational approach aiming to unravel the links between the insect brain and the complex behaviours they display, as well as computational and methodological tools to help and inspire other, future modelling efforts. We tackled notably how several vector-based navigational strategies could be implemented in the *Central Complex* brain area. We also focused on how the *Mushroom Bodies* area can encode a large number of complex views to allow view-based guidance. Taken together, these results provide insights into various questions regarding insect navigation, notably about the existence of a ‘cognitive map’ in insects, or how complexity may emerge from simplicity. I will discuss these here in turns.

5.1 A cognitive map?

To navigate, humans rely generally on computationally expensive (both mentally or technologically) solutions tailored to their own rationality and their own available sensory information. And, observing the impressive navigational feats displayed by insects in complex natural environments, one may wonder if insects rely on similar higher-level spatial representations of their environment. One of the recurring and ongoing debates in insect navigation revolves around the question of whether insects possess, just like us and other mammals, a so-called ‘cognitive map’ [287, 77].

Even if it is difficult (and perhaps impossible) to conceptualize other animals’ mental processes without putting a bit of our own human thoughts in the mix, one must try not to articulate hypotheses which are too anthropomorphic [332, 297]. A question that could be asked instead is whether animals actually need cognitive maps [34].

The modelling studies presented in this thesis demonstrate that certain simple computations, which can be distributed over several brain areas, can indeed explain the emergence of complex behaviours. For instance, the model presented in chapter 1 suggests a plausible mechanism for vector memory addition and subtraction in the insect

brain, which is sufficient for these seemingly complex behaviours to appear. This work shows therefore that vector manipulation is a highly parsimonious explanation, and that the known architecture of the Central Complex is equipped to perform such allocentric encoding and vector operations. Notably, several of the behaviours captured by the model (namely, de-novo shortcutting and multi-location routes ontogeny) are typically assumed to be the signature of the existence of a cognitive map [161, 163]. Similarly, the Mushroom Bodies model presented in chapter 3 and chapter 4 allows homing from remote unknown locations in a complex environment, a behaviour which has also been argued to account for the existence of a map-like representation [82].

What is of particular interest, is the fact that only using known (or very plausible) neural circuitry is sufficient to make these behaviours emerge. This suggests that we may get closer to the understanding of some of the computations these brains perform. Thus, another question arises: since these identified circuits seem to be enough to reproduce the behaviours assumed to be signatures of a cognitive map, does it mean that this circuitry actually holds a cognitive map? In fact, these circuits can be seen on a spectrum of information fragmentation where the more fusion of information there is, the more ‘map-like’ the circuit can be [34].

To illustrate the question, Webb [299] pointed out that recent observations of ants being able to keep an appropriate bearing while walking backwards [6, 250, 251] could be considered as resulting from a higher-order representation, fusing together the information provided by both the view-based and the vector-based representations – or, in other words, from a map-like representation. But the model presented in chapter 4, predicts that the much simpler process of encoding views with a repulsive valence is sufficient to allow homing while walking backwards, without the need of a high-order map representation. This prediction seems to be also verified by behavioural observations [251].

Whether the insect Central Complex, or Mushroom Bodies (or both together) can actually accommodate a cognitive map representation is therefore yet to be demonstrated. It is however absolutely possible that some more complex processes still elude us, and which would need to be incorporated our current models for them to represent a ‘cognitive map’.

5.2 Complexity emerging from simplicity

As exposed in this thesis (see chapter 5) computational modelling is a great tool to tackle the multi-level problematic of how the brain produces behaviour. The power of modelling lays into the intermediary ‘computation’ level [157]. Instead of establishing direct links between the neurons and the behaviour, computational models benefit more

from considering two transitions: the link between neurons and these computations and the link between computations and behaviour.

For instance, chapter 3 shows that the addition of few visual pre-processing steps along the optic pathways upstream of the Mushroom Bodies can allow for encoding view memories efficiently, reusing the sparse encoding process previously described for olfactory memories. This demonstrates that small changes on the circuit level can drastically change the computation level, allowing a holistic encoding of complex views in the Mushroom Bodies (which in turn enables view-based navigation) with little to no additional computational cost. As another example, in the Path Integration model based on the Central Complex connectivity [271], the Systematic Search behavioural routine readily emerges from the circuit even without being explicitly implemented. Furthermore, the addition of a few neurons downstream of the Path Integration circuit (chapter 1) can readily allow the emergence of even more sophisticated vector-based navigational behaviours: storing and recalling vectors memories to return to food sources, take novel shortcuts, perform systematic searches at the feeder and re-calibrate their vector memories with experience. All that without compromising the original Path Integration functionality.

Similarly, we saw in chapter 3 how incorporating a simple but well-known neural aspect to our model can drastically improve navigational behaviour, even though this neural aspect was discovered through the study of olfactory associative learning, an entirely different context compared to navigation. Also, in chapter 4, actively learning, and then combining appetitive and aversive memories [38] of attractive and repulsive views taken in opposite directions [126], allows the model to encode familiarity. With this simple addition at the behavioural level and no drastic circuit changes, it is possible to change the computation level and provide a measurement of the current directional error at any time. In other words, the model is able to measure ‘how much to turn’ from an unfamiliar view without the need to scan and compare the familiarity across multiple directions, thus solving a long-standing ambiguity. Such interactions between attractive and repulsive views have been shown to be a plausible mechanism in ants to avoid traps and enabling detours [336], which illustrates well how the same neural computation can have consequences on several different behaviours.

Taken together, these results emphasise that there is no direct causal relationship between the neural hardware and a given behaviour but a (perhaps rather chaotic) complex regime of interactions.

5.3 Drawing predictions

The purpose of modelling is manifold. It allows us to explore the complex set of interactions between the brain, environment and body through simulations, which unlocks the possibility to get an actual mechanistical understanding of how behaviour emerges. Also importantly, it generates predictions for both the neuroanatomical and behavioural levels, which can be in turn experimentally verified. In the hopes that this work stimulates future research endeavours, I summarise here the main predictions stemming from the various models presented in this thesis.

- A 'vector-memory' neuron could exist in the form of a large inhibitory neuron projecting to all wedges of the CX path integrator output. Similar inhibitory neurons have been identified in *Drosophila* [135].
- 'Recalibration' neurons could exist, triggering synaptic modulation of the vector memory neurons by food-associated reinforcement. Likely candidates for such neurons are dopaminergic neurons (DAN) [142] or octopaminergic neurons (OAN) [327]. Both of these types of neurons are known to project into the CX. Thus, there would be a possibility of experimentally disturbing the formation of these vector memories by inhibiting long-term synaptic changes [e.g., 33]
- The low resolution of insect eyes, and the pooling of multiple facets in a way that allows filtering specific characteristics of the view (i.e., edges extraction, and potentially rotation-independent features) is not only sufficient but beneficial for navigation in complex environments, and should prove useful for robotic applications using real-world visual information.
- The sparse coding in the MBs provides more than enough storage space for encoding long routes in cluttered environments, and importantly the rate at which these views are learnt is directly controlled by the novelty of the views, suggesting a constant latent learning.
- The effective measurement of the directional error at the exact nest location should (counter-intuitively) be similar to the one in completely unfamiliar environments. Indeed, at the exact nest location both attractive and aversive pathways are highly activated because of the many views that have been learnt around the nest. Therefore, these two pathways cancel each other out. In an unfamiliar location, the two pathways are weakly activated because no views are familiar, but they still cancel each other out. The displayed behaviour should therefore be similar in these two conditions. We recently verified this prediction with ants tethered on an air suspended treadmill (see appendix appendix A).

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- Swapping the respective valences of the attractive and aversive pathways should allow to use the same memorised views for inbound or outbound conditions. This could therefore be under the control of a motivational state. This would mean that ants in the ‘homing’ motivation state should be repulsed by the outbound views, and vice versa. Such switch between motivational states (outbound vs. inbound) could be achieved by different DAN/MBON pairs.
 - Two reinforcement signals, categorising whether views should be learnt as aversive or appetitive could exist. These signals may thus be implemented as ‘reinforcer neurons’, which could exist as DANs conveying signals from the LALs to the Mushroom Bodies, and they could be under the control of the Path Integrator.
 - In principle, it should be possible to selectively silence these attractive and aversive ‘reinforcers neurons’ pharmacologically with a specific receptor (such as GABA) antagonist in the output region of the MBONs.

The increasing knowledge about insects’ neural circuitry [117, 105, 1, 237, 92] is a fantastic opportunity to formulate new bio-inspired models, especially in light of computational approaches. The parametrisation possibilities (synaptic dynamics, neurons adaptation, etc) and number of cells groups that can be included in future modelling efforts, according to what we observe in the brain, is increasing every day. The computational tools also enable the use of complex 3D environments for simulating navigational tasks (chapter 2). Virtual Reality paradigms provide opportunities to test real animals in a wider range of conditions, further unlocking the variety of behaviours that can be observed and modelled. It also allows us to test real insects and virtual agents in the exact same virtual environments, streamlining the comparative approaches and facilitating predictions testing. These are all reasons why I think the role of computational modelling in neuroethology is only at its beginning.

5.4 Conclusion

When asking if other animals are intelligent or even capable of thinking, us humans often see it as an overarching, multi-purpose ability, often considering themselves as the most endowed ones, lessening other life forms below them. As we have seen through many examples in insect navigation, it is often helpful to steer away from this human-centred point of view and reconsider how we see intelligence. Intelligence is probably not a centralised quantifiable measure, it is very much unique to each individual and deeply interwoven with its unique environment, scale and ecological needs. This thesis (like others before) shows how ‘intelligent behaviour’ can stem from the interaction between

distributed simple computations, including not only the brain but also the body and the environment. From these observations, a tentative definition of intelligence could be the efficiency with which an individual acquires information about its environment (i.e., learns), memorises and integrates this information properly to develop novel responses and behaviours. Indeed, why would it make sense to think about intelligence as a somewhat independent ability enclosed in the individual's brain, when the actual expression of it is only visible through 'intelligent actions'? Does it not appear more sensible to think that the ways brains solve problems fundamentally depends on the context of the body and local environment they are embedded in? [297]

Ethologists like Tinbergen, Thorpe, or von Frisch had a view that was relatively clear regarding social hymenopterans. They valued the role of the body and environment so much that they considered these as the sole sources of explanation for the insect's behavioural repertoires: the actions displayed by these animals would be the results of high adaptations of their body (through specialized sensory organs or motor effectors) and purely instinctive responses to the environment, like some sorts of 'robotic beings'. On the other hand, one may then argue that – putting environment, body, and learning aside – being an intelligent form of life is simply having 'something more': the idea of a mind or soul on top of any physically observable biological property ('subjective beings'). This actually echoes to the classic vision of Descartes of a complete duality between body and mind, a vision nicely coined with the phrase "*a Ghost in the Machine*" by philosopher Gilbert Ryle [235].

Whichever of the two views ('robotic beings' vs. 'subjective beings') gets the closest to reality is definitely not up to this thesis to answer, and from where we stand, either by observing their behaviour or by looking directly at the neural activity, we can only infer what kind of processes are happening in other animals' brains. But this question highlights an important fact: the repertoire of behaviours displayed by insects (and other animals) usually include both of these stereotypical, reflex-like actions as well as experience-dependent plasticity and decision making. In other words, as it is so often the case in biology, the conclusion can be summarised as: "*it's probably a bit of both*".

Thus, understanding the processes happening in the brains and how the neural hardware produces intelligent actions is maybe an over-ambitious project which will probably never be completely achieved but there are many fascinating and often very humbling discoveries to be made along the way.

Bibliography

- [1] Andrea Adden et al. “The Brain of a Nocturnal Migratory Insect, the Australian Bogong Moth”. In: *Journal of Comparative Neurology* 528.11 (2020), pp. 1942–1963. ISSN: 1096-9861. DOI: [10.1002/cne.24866](https://doi.org/10.1002/cne.24866).
- [2] Volkan Aksoy and Yilmaz Camlitepe. “Behavioural Analysis of Chromatic and Achromatic Vision in the Ant *Formica Cunicularia* (Hymenoptera: Formicidae)”. In: *Vision Research* 67 (15th Aug. 2012), pp. 28–36. ISSN: 0042-6989. DOI: [10.1016/j.visres.2012.06.013](https://doi.org/10.1016/j.visres.2012.06.013).
- [3] David J. Anderson and Pietro Perona. “Toward a Science of Computational Ethology”. In: *Neuron* 84.1 (1st Oct. 2014), pp. 18–31. ISSN: 0896-6273. DOI: [10.1016/j.neuron.2014.09.005](https://doi.org/10.1016/j.neuron.2014.09.005).
- [4] Paul Ardin et al. “How Variation in Head Pitch Could Affect Image Matching Algorithms for Ant Navigation”. In: *Journal of Comparative Physiology A* 201.6 (June 2015), pp. 585–597. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/s00359-015-1005-8](https://doi.org/10.1007/s00359-015-1005-8).
- [5] Paul Ardin et al. “Using an Insect Mushroom Body Circuit to Encode Route Memory in Complex Natural Environments”. In: *PLoS Computational Biology* 12.2 (11th Feb. 2016). ISSN: 1553-734X. DOI: [10.1371/journal.pcbi.1004683](https://doi.org/10.1371/journal.pcbi.1004683).
- [6] Paul B. Ardin, Michael Mangan and Barbara Webb. “Ant Homing Ability Is Not Diminished When Traveling Backwards”. In: *Frontiers in Behavioral Neuroscience* 10 (13th Apr. 2016). ISSN: 1662-5153. DOI: [10.3389/fnbeh.2016.00069](https://doi.org/10.3389/fnbeh.2016.00069).
- [7] Paolo Arena et al. “A Spiking Network for Spatial Memory Formation: Towards a Fly-Inspired Ellipsoid Body Model”. In: *The 2013 International Joint Conference on Neural Networks (IJCNN)*. The 2013 International Joint Conference on Neural Networks (IJCNN). Aug. 2013, pp. 1–6. DOI: [10.1109/IJCNN.2013.6706882](https://doi.org/10.1109/IJCNN.2013.6706882).
- [8] Yoshinori Aso et al. “Mushroom Body Output Neurons Encode Valence and Guide Memory-Based Action Selection in *Drosophila*”. In: *eLife* 3 (23rd Dec. 2014), e04580. ISSN: 2050-084X. DOI: [10.7554/eLife.04580](https://doi.org/10.7554/eLife.04580).

- [9] Baktash Babadi and Haim Sompolinsky. “Sparseness and Expansion in Sensory Representations”. In: *Neuron* 83.5 (3rd Sept. 2014), pp. 1213–1226. ISSN: 1097-4199. DOI: [10.1016/j.neuron.2014.07.035](https://doi.org/10.1016/j.neuron.2014.07.035).
- [10] Bart Baddeley et al. “A Model of Ant Route Navigation Driven by Scene Familiarity”. In: *PLoS Computational Biology* 8.1 (5th Jan. 2012). Ed. by Holk Cruse, e1002336. ISSN: 1553-7358. DOI: [10.1371/JOURNAL.PCBI.1002336](https://doi.org/10.1371/JOURNAL.PCBI.1002336).
- [11] Bart Baddeley et al. “Holistic Visual Encoding of Ant-like Routes: Navigation without Waypoints”. In: *Adaptive Behavior* (28th Feb. 2011). DOI: [10.1177/1059712310395410](https://doi.org/10.1177/1059712310395410).
- [12] B. Bausenwein, R. Wolf and M. Heisenberg. “Genetic Dissection of Optomotor Behavior in *Drosophila Melanogaster*. Studies on Wild-Type and the Mutant Optomotor-blindH31”. In: *Journal of Neurogenetics* 3.2 (Mar. 1986), pp. 87–109. ISSN: 0167-7063. DOI: [10.3109/01677068609106897](https://doi.org/10.3109/01677068609106897).
- [13] Randall D. Beer. “6 - The Dynamics of Brain–Body–Environment Systems: A Status Report”. In: *Handbook of Cognitive Science*. Ed. by Paco Calvo and Antoni Gomila. Perspectives on Cognitive Science. San Diego: Elsevier, 1st Jan. 2008, pp. 99–120. DOI: [10.1016/B978-0-08-046616-3.00006-2](https://doi.org/10.1016/B978-0-08-046616-3.00006-2).
- [14] Jon Louis Bentley. “Multidimensional Binary Search Trees Used for Associative Searching”. In: *Communications of the ACM* 18.9 (1st Sept. 1975), pp. 509–517. ISSN: 0001-0782. DOI: [10.1145/361002.361007](https://doi.org/10.1145/361002.361007).
- [15] Guy Beugnon and Raymond Campan. “Homing in the Field Cricket, *Gryllus Campestris*”. In: *Journal of Insect Behavior* 2.2 (1st Mar. 1989), pp. 187–198. ISSN: 1572-8889. DOI: [10.1007/BF01053291](https://doi.org/10.1007/BF01053291).
- [16] Tobias Bockhorst and Uwe Homberg. “Amplitude and Dynamics of Polarization-Plane Signaling in the Central Complex of the Locust Brain”. In: *Journal of Neurophysiology* 113.9 (1st May 2015), pp. 3291–3311. ISSN: 1522-1598. DOI: [10.1152/jn.00742.2014](https://doi.org/10.1152/jn.00742.2014).
- [17] Douglas M. Bolzon, Karin Nordström and David C. O’Carroll. “Local and Large-Range Inhibition in Feature Detection”. In: *Journal of Neuroscience* 29.45 (11th Nov. 2009), pp. 14143–14150. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.2857-09.2009](https://doi.org/10.1523/JNEUROSCI.2857-09.2009).
- [18] Seán G. Brady et al. “Evaluating Alternative Hypotheses for the Early Evolution and Diversification of Ants”. In: *Proceedings of the National Academy of Sciences* 103.48 (28th Nov. 2006), pp. 18172–18177. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.0605858103](https://doi.org/10.1073/pnas.0605858103).
- [19] M. L. Brines and J. L. Gould. “Bees Have Rules”. In: *Science* 206.4418 (2nd Nov. 1979), pp. 571–573. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.206.4418.571](https://doi.org/10.1126/science.206.4418.571).

-
- [20] Cornelia Buehlmann, Alexia Aussel and Paul Graham. “Dynamic Multimodal Interactions in Navigating Wood Ants: What Do Path Details Tell Us about Cue Integration?” In: *Journal of Experimental Biology* 223 (jeb221036 3rd Apr. 2020). ISSN: 0022-0949. DOI: [10.1242/jeb.221036](https://doi.org/10.1242/jeb.221036).
- [21] Cornelia Buehlmann, Bill S. Hansson and Markus Knaden. “Flexible Weighing of Olfactory and Vector Information in the Desert Ant *Cataglyphis Fortis*”. In: *Biology Letters* 9.3 (23rd June 2013), p. 20130070. DOI: [10.1098/rsbl.2013.0070](https://doi.org/10.1098/rsbl.2013.0070).
- [22] Cornelia Buehlmann et al. “Desert Ants Locate Food by Combining High Sensitivity to Food Odors with Extensive Crosswind Runs”. In: *Current Biology* 24.9 (5th May 2014), pp. 960–964. ISSN: 0960-9822. DOI: [10.1016/j.cub.2014.02.056](https://doi.org/10.1016/j.cub.2014.02.056).
- [23] Cornelia Buehlmann et al. “Desert Ants Use Olfactory Scenes for Navigation”. In: *Animal Behaviour* 106 (1st Aug. 2015), pp. 99–105. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2015.04.029](https://doi.org/10.1016/j.anbehav.2015.04.029).
- [24] Cornelia Buehlmann et al. “Mushroom Bodies Are Required for Learned Visual Navigation, but Not for Innate Visual Behavior, in Ants”. In: *Current Biology* 30.17 (7th Sept. 2020), 3438–3443.e2. ISSN: 0960-9822. DOI: [10.1016/j.cub.2020.07.013](https://doi.org/10.1016/j.cub.2020.07.013).
- [25] Cornelia Bühlmann, Ken Cheng and Rüdiger Wehner. “Vector-Based and Landmark-Guided Navigation in Desert Ants Inhabiting Landmark-Free and Landmark-Rich Environments”. In: *Journal of Experimental Biology* 214.17 (1st Sept. 2011), pp. 2845–2853. ISSN: 0022-0949. DOI: [10.1242/jeb.054601](https://doi.org/10.1242/jeb.054601).
- [26] Amélie Cabirol et al. “Relationship between Brain Plasticity, Learning and Foraging Performance in Honey Bees”. In: *PLOS ONE* 13.4 (30th Apr. 2018). Ed. by Olav Rueppell, e0196749. ISSN: 1932-6203. DOI: [10.1371/JOURNAL.PONE.0196749](https://doi.org/10.1371/JOURNAL.PONE.0196749).
- [27] Josep Calbó, David Pagès and Josep-Abel González. “Empirical Studies of Cloud Effects on UV Radiation: A Review”. In: *Reviews of Geophysics* 43.2 (2005). ISSN: 1944-9208. DOI: [10.1029/2004RG000155](https://doi.org/10.1029/2004RG000155).
- [28] Jessica Cande et al. “Optogenetic Dissection of Descending Behavioral Control in *Drosophila*”. In: *eLife* 7 (26th June 2018). Ed. by Kristin Scott, e34275. ISSN: 2050-084X. DOI: [10.7554/eLife.34275](https://doi.org/10.7554/eLife.34275).
- [29] B. A. Cartwright and T. S. Collett. “Landmark Learning in Bees: Experiments and Models”. In: *Journal of Comparative Physiology ? A* 151.4 (1983), pp. 521–543. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/BF00605469](https://doi.org/10.1007/BF00605469).
- [30] Stijn Cassenaer and Gilles Laurent. “Hebbian STDP in Mushroom Bodies Facilitates the Synchronous Flow of Olfactory Information in Locusts”. In: *Nature* 448.7154 (Aug. 2007), pp. 709–713. ISSN: 0028-0836, 1476-4687. DOI: [10.1038/NATURE05973](https://doi.org/10.1038/NATURE05973).

- [31] N. Alex Cayco-Gajic and R. Angus Silver. “Re-Evaluating Circuit Mechanisms Underlying Pattern Separation”. In: *Neuron* 101.4 (20th Feb. 2019), pp. 584–602. ISSN: 0896-6273. DOI: [10.1016/j.neuron.2019.01.044](https://doi.org/10.1016/j.neuron.2019.01.044).
- [32] Xim Cerdá and Javier Retana. “Alternative Strategies by Thermophilic Ants to Cope with Extreme Heat: Individual versus Colony Level Traits”. In: *Oikos* 89.1 (2000), pp. 155–163. ISSN: 0030-1299. JSTOR: [3547459](https://www.jstor.org/stable/3547459).
- [33] Chun-Chao Chen et al. “Visualizing Long-Term Memory Formation in Two Neurons of the *Drosophila* Brain”. In: *science* 335.6069 (2012), pp. 678–685. DOI: [10.1126/science.1212735](https://doi.org/10.1126/science.1212735).
- [34] Allen Cheung et al. “Maintaining a Cognitive Map in Darkness: The Need to Fuse Boundary Knowledge with Path Integration”. In: *PLoS Computational Biology* 8.8 (16th Aug. 2012). ISSN: 1553-734X. DOI: [10.1371/journal.pcbi.1002651](https://doi.org/10.1371/journal.pcbi.1002651).
- [35] Lars Chittka and Jeremy Niven. “Are Bigger Brains Better?” In: *Current Biology* 19.21 (17th Nov. 2009), R995–R1008. ISSN: 0960-9822. DOI: [10.1016/j.cub.2009.08.023](https://doi.org/10.1016/j.cub.2009.08.023).
- [36] Keith A. Christian and Stephen R. Morton. “Extreme Thermophilia in a Central Australian Ant, *Melophorus Bagoti*”. In: *Physiological Zoology* 65.5 (1992), pp. 885–905. ISSN: 0031-935X. JSTOR: [30158548](https://www.jstor.org/stable/30158548).
- [37] Andy Clark. *Being There: Putting Brain, Body, and World Together Again*. MIT Press, 23rd Jan. 1998. 310 pp. ISBN: 978-0-262-26052-7. Google Books: [i03NKyOm11gC](https://books.google.com/books?id=i03NKyOm11gC).
- [38] Paola Cognigni, Johannes Felsenberg and Scott Waddell. “Do the Right Thing: Neural Network Mechanisms of Memory Formation, Expression and Update in *Drosophila*”. In: *Current Opinion in Neurobiology*. *Neurobiology of Behavior* 49 (1st Apr. 2018), pp. 51–58. ISSN: 0959-4388. DOI: [10.1016/j.conb.2017.12.002](https://doi.org/10.1016/j.conb.2017.12.002).
- [39] Matthew Collett, Lars Chittka and Thomas S. Collett. “Spatial Memory in Insect Navigation”. In: *Current biology: CB* 23.17 (9th Sept. 2013), R789–800. ISSN: 1879-0445. DOI: [10.1016/j.cub.2013.07.020](https://doi.org/10.1016/j.cub.2013.07.020).
- [40] Matthew Collett, Thomas S Collett and Rüdiger Wehner. “Calibration of Vector Navigation in Desert Ants”. In: *Current Biology* 9.18 (1999), 1031–S1. DOI: [10.1016/S0960-9822\(99\)80451-5](https://doi.org/10.1016/S0960-9822(99)80451-5).
- [41] T. S. Collett and J. Baron. “Biological Compasses and the Coordinate Frame of Landmark Memories in Honeybees”. In: *Nature* 368.6467 (6467 Mar. 1994), pp. 137–140. ISSN: 1476-4687. DOI: [10.1038/368137a0](https://doi.org/10.1038/368137a0).
- [42] T. S. Collett and J. Zeil. “The Selection and Use of Landmarks by Insects”. In: *Orientation and Communication in Arthropods*. Ed. by Miriam Lehrer. EXS. Basel: Birkhäuser, 1997, pp. 41–65. ISBN: 978-3-0348-8878-3. DOI: [10.1007/978-3-0348-8878-3_2](https://doi.org/10.1007/978-3-0348-8878-3_2).

-
- [43] T. S. Collett et al. “Landmark Learning and Guidance in Insects”. In: *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 337.1281 (29th Sept. 1992), pp. 295–303. DOI: [10.1098/rstb.1992.0107](https://doi.org/10.1098/rstb.1992.0107).
- [44] Thomas S Collett and Matthew Collett. “Path Integration in Insects”. In: *Current Opinion in Neurobiology* 10.6 (1st Dec. 2000), pp. 757–762. ISSN: 0959-4388. DOI: [10.1016/S0959-4388\(00\)00150-1](https://doi.org/10.1016/S0959-4388(00)00150-1).
- [45] Thomas S. Collett and Matthew Collett. “Memory Use in Insect Visual Navigation”. In: *Nature Reviews Neuroscience* 3.7 (July 2002), pp. 542–552. ISSN: 1471-003X, 1471-0048. DOI: [10.1038/nrn872](https://doi.org/10.1038/nrn872).
- [46] Thomas S. Collett and Jochen Zeil. “Insect Learning Flights and Walks”. In: *Current biology: CB* 28.17 (10th Sept. 2018), R984–R988. ISSN: 1879-0445. DOI: [10.1016/j.cub.2018.04.050](https://doi.org/10.1016/j.cub.2018.04.050).
- [47] TS Collett, P Graham and RA Harris. “Novel Landmark-Guided Routes in Ants”. In: *Journal of Experimental Biology* 210.12 (2007), pp. 2025–2032. DOI: [10.1242/jeb.000315](https://doi.org/10.1242/jeb.000315).
- [48] Blender Online Community. *Blender - a 3D Modelling and Rendering Package*. Stichting Blender Foundation, Amsterdam: Blender Foundation, 2018. URL: <http://www.blender.org>.
- [49] Victor Cornetz. “Album faisant suite aux Trajets de fourmis et retours au nid”. In: (1910).
- [50] Holk Cruse and Rüdiger Wehner. “No Need for a Cognitive Map: Decentralized Memory for Insect Navigation”. In: *PLOS Computational Biology* 7.3 (17th Mar. 2011), e1002009. ISSN: 1553-7358. DOI: [10.1371/journal.pcbi.1002009](https://doi.org/10.1371/journal.pcbi.1002009).
- [51] Charles Darwin. *The Descent of Man, and Selection in Relation to Sex, Vol. 1*. London, England: John Murray, 1871, pp. viii, 423. viii, 423. DOI: [10.1037/12293-000](https://doi.org/10.1037/12293-000).
- [52] Jacqueline Degen et al. “Exploratory Behaviour of Honeybees during Orientation Flights”. In: *Animal Behaviour* 102 (1st Apr. 2015), pp. 45–57. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2014.12.030](https://doi.org/10.1016/j.anbehav.2014.12.030).
- [53] Jean-Marc Devaud et al. “Neural Substrate for Higher-Order Learning in an Insect: Mushroom Bodies Are Necessary for Configural Discriminations”. In: *Proceedings of the National Academy of Sciences* 112.43 (27th Oct. 2015), E5854–E5862. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.1508422112](https://doi.org/10.1073/pnas.1508422112).
- [54] Alex DM Dewar, Andrew Philippides and Paul Graham. “What Is the Relationship between Visual Environment and the Form of Ant Learning-Walks? An in Silico Investigation of Insect Navigation”. In: *Adaptive Behavior* 22.3 (1st June 2014), pp. 163–179. ISSN: 1059-7123. DOI: [10.1177/1059712313516132](https://doi.org/10.1177/1059712313516132).

- [55] Dario Differt and Ralf Möller. “Insect Models of Illumination-Invariant Skyline Extraction from UV and Green Channels”. In: *Journal of Theoretical Biology* 380 (Sept. 2015), pp. 444–462. ISSN: 00225193. DOI: [10.1016/j.jtbi.2015.06.020](https://doi.org/10.1016/j.jtbi.2015.06.020).
- [56] Jeffrey M. Donlea, Diogo Pimentel and Gero Miesenböck. “Neuronal Machinery of Sleep Homeostasis in *Drosophila*”. In: *Neuron* 81.4 (19th Feb. 2014), pp. 860–872. ISSN: 0896-6273. DOI: [10.1016/j.neuron.2013.12.013](https://doi.org/10.1016/j.neuron.2013.12.013).
- [57] John K. Douglass and Nicholas J. Strausfeld. “Functionally and Anatomically Segregated Visual Pathways in the Lobula Complex of a Calliphorid Fly”. In: *The Journal of Comparative Neurology* 396.1 (22nd June 1998), pp. 84–104. ISSN: 0021-9967, 1096-9861. DOI: [10.1002/\(SICI\)1096-9861\(19980622\)396:1<84::AID-CNE7>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1096-9861(19980622)396:1<84::AID-CNE7>3.0.CO;2-E).
- [58] Peter Duelli and Rüdiger Wehner. “The Spectral Sensitivity of Polarized Light Orientation in *Cataglyphis Bicolor* (Formicidae, Hymenoptera)”. In: *Journal of Comparative Physiology A* 86.1 (1st Mar. 1973), pp. 37–53. ISSN: 1432-1351. DOI: [10.1007/BF00694476](https://doi.org/10.1007/BF00694476).
- [59] Virginie Durier and Colette Rivault. “Path Integration in Cockroach Larvae, *Blattella Germanica* (L.) (Insect : Dictyoptera): Direction and Distance Estimation”. In: *Animal Learning and Behaviour* 27.1 (Mar. 1999), pp. 108–118. DOI: [10.3758/BF03199436](https://doi.org/10.3758/BF03199436).
- [60] Olga Dyakova et al. “Image Statistics of the Environment Surrounding Freely Behaving Hoverflies”. In: *Journal of Comparative Physiology A* 205.3 (1st June 2019), pp. 373–385. ISSN: 1432-1351. DOI: [10.1007/s00359-019-01329-1](https://doi.org/10.1007/s00359-019-01329-1).
- [61] Birgit Ehmer and Wulfila Gronenberg. “Mushroom Body Volumes and Visual Interneurons in Ants: Comparison between Sexes and Castes”. In: *The Journal of Comparative Neurology* 469.2 (2nd Feb. 2004), pp. 198–213. ISSN: 0021-9967. DOI: [10.1002/cne.11014](https://doi.org/10.1002/cne.11014).
- [62] Birgit Ehmer and Wulfila Gronenberg. “Segregation of Visual Input to the Mushroom Bodies in the Honeybee (*Apis Mellifera*)”. In: *The Journal of Comparative Neurology* 451.4 (30th Sept. 2002), pp. 362–373. ISSN: 0021-9967, 1096-9861. DOI: [10.1002/CNE.10355](https://doi.org/10.1002/CNE.10355).
- [63] Katharina Eichler et al. “The Complete Connectome of a Learning and Memory Centre in an Insect Brain”. In: *Nature* 548.7666 (9th Aug. 2017), pp. 175–182. ISSN: 0028-0836, 1476-4687. DOI: [10.1038/NATURE23455](https://doi.org/10.1038/NATURE23455).
- [64] Basil el Jundi et al. “Spectral Information as an Orientation Cue in Dung Beetles”. In: *Biology Letters* 11.11 (Nov. 2015), p. 20150656. ISSN: 1744-9561, 1744-957X. DOI: [10.1098/rsbl.2015.0656](https://doi.org/10.1098/rsbl.2015.0656).

-
- [65] Jean-Henri Fabre. *Nouveaux souvenirs entomologiques: études sur l'instinct et les mœurs des insectes*. Paris: Librairie Ch. Delagrave, 1882. 376 pp. Google Books: [RTwIAQAAIAAJ](#).
- [66] S. E. Fahrbach et al. “Expansion of the Neuropil of the Mushroom Bodies in Male Honey Bees Is Coincident with Initiation of Flight”. In: *Neuroscience Letters* 236.3 (7th Nov. 1997), pp. 135–138. ISSN: 0304-3940. DOI: [10.1016/s0304-3940\(97\)00772-6](#).
- [67] Susan E. Fahrbach. “Structure of the Mushroom Bodies of the Insect Brain”. In: *Annual Review of Entomology* 51.1 (2006), pp. 209–232. DOI: [10.1146/annurev.ento.51.110104.150954](#).
- [68] Sarah M. Farris and Susanne Schulmeister. “Parasitoidism, Not Sociality, Is Associated with the Evolution of Elaborate Mushroom Bodies in the Brains of Hymenopteran Insects”. In: *Proceedings. Biological Sciences* 278.1707 (22nd Mar. 2011), pp. 940–951. ISSN: 1471-2954. DOI: [10.1098/rspb.2010.2161](#).
- [69] Sarah M. Farris and Irina Sinakevitch. “Development and Evolution of the Insect Mushroom Bodies: Towards the Understanding of Conserved Developmental Mechanisms in a Higher Brain Center”. In: *Arthropod Structure & Development* 32.1 (Aug. 2003), pp. 79–101. ISSN: 14678039. DOI: [10.1016/S1467-8039\(03\)00009-4](#).
- [70] Pauline N. Fleischmann et al. “Ontogeny of Learning Walks and the Acquisition of Landmark Information in Desert Ants, *Cataglyphis Fortis*”. In: *The Journal of Experimental Biology* 219.19 (1st Oct. 2016), pp. 3137–3145. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.140459](#).
- [71] Pauline N. Fleischmann et al. “Species-Specific Differences in the Fine Structure of Learning Walk Elements in *Cataglyphis* Ants”. In: *Journal of Experimental Biology* 220.13 (1st July 2017), pp. 2426–2435. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.158147](#).
- [72] Pauline Nikola Fleischmann, Wolfgang Rössler and Rüdiger Wehner. “Early Foraging Life: Spatial and Temporal Aspects of Landmark Learning in the Ant *Cataglyphis Noda*”. In: *Journal of Comparative Physiology A* 204.6 (June 2018), pp. 579–592. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/S00359-018-1260-6](#).
- [73] Dario Floreano et al. “Miniature Curved Artificial Compound Eyes”. In: *Proceedings of the National Academy of Sciences* 110.23 (4th June 2013), pp. 9267–9272. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.1219068110](#).
- [74] Vincent Fourcassié. “Landmark Orientation in Natural Situations in the Red Wood Ant *Formica Lugubris* Zett. (Hymenoptera Formicidae)”. In: *Ethology Ecology & Evolution* 3.2 (1st May 1991), pp. 89–99. ISSN: 0394-9370. DOI: [10.1080/08927014.1991.9525376](#).

- [75] Matthias O. Franz et al. “Learning View Graphs for Robot Navigation”. In: *Autonomous Robots* 5.1 (1st Mar. 1998), pp. 111–125. ISSN: 1573-7527. DOI: [10.1023/A:1008821210922](https://doi.org/10.1023/A:1008821210922).
- [76] Cody A. Freas et al. “The View from the Trees: Nocturnal Bull Ants, *Myrmecia Midas*, Use the Surrounding Panorama While Descending from Trees”. In: *Frontiers in psychology* 9 (2018), p. 16. DOI: [10.3389/fpsyg.2018.00016](https://doi.org/10.3389/fpsyg.2018.00016).
- [77] Charles R. Gallistel. *The Organization of Learning*. The Organization of Learning. Cambridge, MA, US: The MIT Press, 1990, pp. viii, 648. viii, 648. ISBN: 978-0-262-07113-0.
- [78] W. J. Gehring and R. Wehner. “Heat Shock Protein Synthesis and Thermotolerance in *Cataglyphis*, an Ant from the Sahara Desert.” In: *Proceedings of the National Academy of Sciences* 92.7 (28th Mar. 1995), pp. 2994–2998. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.92.7.2994](https://doi.org/10.1073/pnas.92.7.2994).
- [79] Ysabel Milton Giraldo et al. “Sun Navigation Requires Compass Neurons in *Drosophila*”. In: *Current Biology* 28.17 (10th Sept. 2018), 2845–2852.e4. ISSN: 0960-9822. DOI: [10.1016/j.cub.2018.07.002](https://doi.org/10.1016/j.cub.2018.07.002).
- [80] Dennis Goldschmidt, Poramate Manoonpong and Sakyasingha Dasgupta. “A Neurocomputational Model of Goal-Directed Navigation in Insect-Inspired Artificial Agents”. In: *Frontiers in Neurobotics* 11 (2017), p. 20. ISSN: 1662-5218. DOI: [10.3389/fnbot.2017.00020](https://doi.org/10.3389/fnbot.2017.00020).
- [81] Alex Gomez-Marin and Asif A. Ghazanfar. “The Life of Behavior”. In: *Neuron* 104.1 (9th Oct. 2019), pp. 25–36. ISSN: 0896-6273. DOI: [10.1016/j.neuron.2019.09.017](https://doi.org/10.1016/j.neuron.2019.09.017).
- [82] J. L. Gould. “The Locale Map of Honey Bees: Do Insects Have Cognitive Maps?” In: *Science (New York, N.Y.)* 232.4752 (16th May 1986), pp. 861–863. ISSN: 0036-8075. DOI: [10.1126/science.232.4752.861](https://doi.org/10.1126/science.232.4752.861).
- [83] P. Graham, A. Philippides and B. Baddeley. “Animal Cognition: Multi-Modal Interactions in Ant Learning”. In: *Current Biology* 20.15 (2010-08, 2010-8), R639–R640. ISSN: 0960-9822. DOI: [10.1016/j.cub.2010.06.018](https://doi.org/10.1016/j.cub.2010.06.018).
- [84] Paul Graham and Ken Cheng. “Ants Use the Panoramic Skyline as a Visual Cue during Navigation”. In: *Current Biology* 19.20 (Nov. 2009), R935–R937. ISSN: 09609822. DOI: [10.1016/j.cub.2009.08.015](https://doi.org/10.1016/j.cub.2009.08.015).
- [85] Paul Graham and Ken Cheng. “Which Portion of the Natural Panorama Is Used for View-Based Navigation in the Australian Desert Ant?” In: *Journal of Comparative Physiology A* 195.7 (29th Apr. 2009), p. 681. ISSN: 1432-1351. DOI: [10.1007/s00359-009-0443-6](https://doi.org/10.1007/s00359-009-0443-6).

-
- [86] Paul Graham and Thomas S. Collett. “View-Based Navigation in Insects: How Wood Ants (*Formica rufa*L.) Look at and Are Guided by Extended Landmarks”. In: *Journal of Experimental Biology* 205.16 (15th Aug. 2002), pp. 2499–2509. ISSN: 0022-0949. DOI: [10.1242/jeb.205.16.2499](https://doi.org/10.1242/jeb.205.16.2499).
- [87] Paul Graham, Karine Fauria and Thomas S. Collett. “The Influence of Beacon-Aiming on the Routes of Wood Ants”. In: *Journal of Experimental Biology* 206.3 (1st Feb. 2003), pp. 535–541. ISSN: 1477-9145, 0022-0949. DOI: [10.1242/jeb.00115](https://doi.org/10.1242/jeb.00115).
- [88] Jonathan Green et al. “A Neural Circuit Architecture for Angular Integration in *Drosophila*”. In: *Nature* 546.7656 (22nd May 2017), pp. 101–106. ISSN: 0028-0836, 1476-4687. DOI: [10.1038/NATURE22343](https://doi.org/10.1038/NATURE22343).
- [89] Robin Grob et al. “The Role of Celestial Compass Information in *Cataglyphis* Ants during Learning Walks and for Neuroplasticity in the Central Complex and Mushroom Bodies”. In: *Frontiers in Behavioral Neuroscience* 11 (14th Nov. 2017). ISSN: 1662-5153. DOI: [10.3389/FNBEH.2017.00226](https://doi.org/10.3389/FNBEH.2017.00226).
- [90] W. Gronenberg. “Subdivisions of Hymenopteran Mushroom Body Calyces by Their Afferent Supply”. In: *The Journal of Comparative Neurology* 435.4 (9th July 2001), pp. 474–489. ISSN: 0021-9967. DOI: [10.1002/cne.1045](https://doi.org/10.1002/cne.1045).
- [91] Alfred Haar. “Zur Theorie der orthogonalen Funktionensysteme”. In: *Mathematische Annalen* 69.3 (1st Sept. 1910), pp. 331–371. ISSN: 1432-1807. DOI: [10.1007/BF01456326](https://doi.org/10.1007/BF01456326).
- [92] Jens Habenstein et al. “The Brain of *Cataglyphis* Ants: Neuronal Organization and Visual Projections”. In: *Journal of Comparative Neurology* 528.18 (2020), pp. 3479–3506. ISSN: 1096-9861. DOI: [10.1002/cne.24934](https://doi.org/10.1002/cne.24934).
- [93] Thomas Haferlach et al. “Evolving a Neural Model of Insect Path Integration”. In: *Adaptive Behavior* 15.3 (Sept. 2007), pp. 273–287. ISSN: 1059-7123, 1741-2633. DOI: [10.1177/1059712307082080](https://doi.org/10.1177/1059712307082080).
- [94] Verena Vanessa Hafner. “Adaptive Homing—Robotic Exploration Tours”. In: *Adaptive Behavior* 9.3-4 (Sept. 2001), pp. 131–141. ISSN: 1059-7123, 1741-2633. DOI: [10.1177/10597123010093002](https://doi.org/10.1177/10597123010093002).
- [95] Martin Hammer. “An Identified Neuron Mediates the Unconditioned Stimulus in Associative Olfactory Learning in Honeybees”. In: *Nature* 366.6450 (6450 Nov. 1993), pp. 59–63. ISSN: 1476-4687. DOI: [10.1038/366059a0](https://doi.org/10.1038/366059a0).
- [96] U. Hanesch, K. -F. Fischbach and M. Heisenberg. “Neuronal Architecture of the Central Complex in *Drosophila Melanogaster*”. In: *Cell and Tissue Research* 257.2 (1989), pp. 343–366. ISSN: 0302-766X, 1432-0878. DOI: [10.1007/BF00261838](https://doi.org/10.1007/BF00261838).

- [97] Walter Hangartner. “Spezifität und Inaktivierung des Spurpheromons von *Lasius fuliginosus* Latr. und Orientierung der Arbeiterinnen im Duftfeld”. In: *Zeitschrift für vergleichende Physiologie* 57.2 (1st June 1967), pp. 103–136. ISSN: 1432-1351. DOI: [10.1007/BF00303068](https://doi.org/10.1007/BF00303068).
- [98] Ben J. Hardcastle et al. “A Visual Pathway for Skylight Polarization Processing in *Drosophila*”. In: *eLife* 10 (23rd Mar. 2021). ISSN: 2050-084X. DOI: [10.7554/eLife.63225](https://doi.org/10.7554/eLife.63225).
- [99] C. M. Harley and R. E. Ritzmann. “Electrolytic Lesions within Central Complex Neuropils of the Cockroach Brain Affect Negotiation of Barriers”. In: *The Journal of Experimental Biology* 213 (Pt 16 15th Aug. 2010), pp. 2851–2864. ISSN: 1477-9145. DOI: [10.1242/jeb.042499](https://doi.org/10.1242/jeb.042499).
- [100] S. Heinze, S. Gotthardt and U. Homberg. “Transformation of Polarized Light Information in the Central Complex of the Locust”. In: *Journal of Neuroscience* 29.38 (23rd Sept. 2009), pp. 11783–11793. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.1870-09.2009](https://doi.org/10.1523/JNEUROSCI.1870-09.2009).
- [101] S. Heinze and U. Homberg. “Maplike Representation of Celestial E-Vector Orientations in the Brain of an Insect”. In: *Science* 315.5814 (16th Feb. 2007), pp. 995–997. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/SCIENCE.1135531](https://doi.org/10.1126/SCIENCE.1135531).
- [102] Stanley Heinze and Uwe Homberg. “Neuroarchitecture of the Central Complex of the Desert Locust: Intrinsic and Columnar Neurons”. In: *The Journal of Comparative Neurology* 511.4 (1st Dec. 2008), pp. 454–478. ISSN: 00219967, 10969861. DOI: [10.1002/CNE.21842](https://doi.org/10.1002/CNE.21842).
- [103] Stanley Heinze, Ajay Narendra and Allen Cheung. “Principles of Insect Path Integration”. In: *Current Biology* 28.17 (10th Sept. 2018), R1043–R1058. ISSN: 0960-9822. DOI: [10.1016/j.cub.2018.04.058](https://doi.org/10.1016/j.cub.2018.04.058).
- [104] Stanley Heinze and Steven M. Reppert. “Sun Compass Integration of Skylight Cues in Migratory Monarch Butterflies”. In: *Neuron* 69.2 (Jan. 2011), pp. 345–358. ISSN: 08966273. DOI: [10.1016/J.NEURON.2010.12.025](https://doi.org/10.1016/J.NEURON.2010.12.025).
- [105] Stanley Heinze et al. “InsectBrainDatabase - A Unified Platform to Manage, Share, and Archive Morphological and Functional Data”. In: *bioRxiv* (1st Dec. 2020), p. 2020.11.30.397489. DOI: [10.1101/2020.11.30.397489](https://doi.org/10.1101/2020.11.30.397489).
- [106] Martin Heisenberg. “Mushroom Body Memoir: From Maps to Models”. In: *Nature Reviews Neuroscience* 4.4 (4 Apr. 2003), pp. 266–275. ISSN: 1471-0048. DOI: [10.1038/nrn1074](https://doi.org/10.1038/nrn1074).
- [107] Martin Heisenberg. “What Do the Mushroom Bodies Do for the Insect Brain? An Introduction”. In: *Learning & Memory* 5.1 (May 1998), pp. 1–10. ISSN: 1072-0502. URL: <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC311238/> (visited on 30/05/2021).

-
- [108] N. Hempel de Ibarra, M. Vorobyev and R. Menzel. “Mechanisms, Functions and Ecology of Colour Vision in the Honeybee”. In: *Journal of Comparative Physiology A* 200.6 (1st June 2014), pp. 411–433. ISSN: 1432-1351. DOI: [10.1007/s00359-014-0915-1](https://doi.org/10.1007/s00359-014-0915-1).
- [109] Natalie Hempel de Ibarra et al. “Preferred Viewing Directions of Bumblebees (*Bombus terrestris*L.) When Learning and Approaching Their Nest Site”. In: *Journal of Experimental Biology* 212.20 (15th Oct. 2009), pp. 3193–3204. ISSN: 0022-0949. DOI: [10.1242/jeb.029751](https://doi.org/10.1242/jeb.029751).
- [110] Cesar A. Hernandez-Reyes et al. “Identification of Exploration and Exploitation Balance in the Silkmoth Olfactory Search Behavior by Information-Theoretic Modeling”. In: *Frontiers in Computational Neuroscience* 15 (1st Feb. 2021). ISSN: 1662-5188. DOI: [10.3389/fncom.2021.629380](https://doi.org/10.3389/fncom.2021.629380).
- [111] Toshihide Hige et al. “Heterosynaptic Plasticity Underlies Aversive Olfactory Learning in *Drosophila*”. In: *Neuron* 88.5 (2nd Dec. 2015), pp. 985–998. ISSN: 1097-4199. DOI: [10.1016/j.neuron.2015.11.003](https://doi.org/10.1016/j.neuron.2015.11.003).
- [112] Mantaro Hironaka et al. “Hierarchical Use of Chemical Marking and Path Integration in the Homing Trip of a Subsocial Shield Bug”. In: *Animal Behaviour* 73.5 (1st May 2007), pp. 739–745. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2006.06.009](https://doi.org/10.1016/j.anbehav.2006.06.009).
- [113] Thierry Hoinville and Rüdiger Wehner. “Optimal Multiguideance Integration in Insect Navigation”. In: *Proceedings of the National Academy of Sciences* 115.11 (13th Mar. 2018), pp. 2824–2829. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.1721668115](https://doi.org/10.1073/pnas.1721668115).
- [114] U. Homberg. “Flight-Related Activity Changes in Neurons of the Lateral Accessory Lobes in the Brain of the Locust *Schistocerca gregaria*”. In: *Journal of Comparative Physiology A* 175.5 (1st Nov. 1994), pp. 597–610. ISSN: 1432-1351. DOI: [10.1007/BF00199481](https://doi.org/10.1007/BF00199481).
- [115] U. Homberg et al. “Central Neural Coding of Sky Polarization in Insects”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 366.1565 (12th Mar. 2011), pp. 680–687. ISSN: 0962-8436, 1471-2970. DOI: [10.1098/RSTB.2010.0199](https://doi.org/10.1098/RSTB.2010.0199).
- [116] Uwe Homberg. “Interneurons of the Central Complex in the Bee Brain (*Apis mellifera*, L.)”. In: *Journal of Insect Physiology* 31.3 (1st Jan. 1985), pp. 251–264. ISSN: 0022-1910. DOI: [10.1016/0022-1910\(85\)90127-1](https://doi.org/10.1016/0022-1910(85)90127-1).
- [117] Anna Honkanen et al. “The Insect Central Complex and the Neural Basis of Navigational Strategies”. In: *Journal of Experimental Biology* 222 (jeb188854 6th Feb. 2019). Ed. by Basil el Jundi, Almut Kelber and Barbara Webb. ISSN: 0022-0949. DOI: [10.1242/jeb.188854](https://doi.org/10.1242/jeb.188854).

- [118] Adrian Horridge. “Pattern Vision of the Honeybee (*Apis Mellifera*): Blue and Green Receptors in the Discrimination of Translocation”. In: *Neurobiology of Learning and Memory* 74.1 (1st July 2000), pp. 1–16. ISSN: 1074-7427. DOI: [10.1006/nlme.1999.3939](https://doi.org/10.1006/nlme.1999.3939).
- [119] Adrian Horridge. “The Spatial Resolutions of the Apposition Compound Eye and Its Neuro-Sensory Feature Detectors: Observation versus Theory”. In: *Journal of Insect Physiology* 51.3 (Mar. 2005), pp. 243–266. ISSN: 00221910. DOI: [10.1016/J.JINSPHYS.2004.11.018](https://doi.org/10.1016/J.JINSPHYS.2004.11.018).
- [120] G. A. Horridge and I. A. Meinertzhagen. “The Accuracy of the Patterns of Connections of the First- and Second-Order Neurons of the Visual System of Calliphora”. In: *Proceedings of the Royal Society of London. Series B, Biological Sciences* 175.1038 (17th Feb. 1970), pp. 69–82. ISSN: 0950-1193. DOI: [10.1098/rspb.1970.0012](https://doi.org/10.1098/rspb.1970.0012).
- [121] George Adrian Horridge. “The Separation of Visual Axes in Apposition Compound Eyes”. In: *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 285.1003 (5th Dec. 1978), pp. 1–59. DOI: [10.1098/rstb.1978.0093](https://doi.org/10.1098/rstb.1978.0093).
- [122] Roman Huber and Markus Knaden. “Egocentric and Geocentric Navigation during Extremely Long Foraging Paths of Desert Ants”. In: *Journal of Comparative Physiology A* 201.6 (1st June 2015), pp. 609–616. ISSN: 1432-1351. DOI: [10.1007/s00359-015-0998-3](https://doi.org/10.1007/s00359-015-0998-3).
- [123] Brad K. Hulse et al. “A Connectome of the *Drosophila* Central Complex Reveals Network Motifs Suitable for Flexible Navigation and Context-Dependent Action Selection”. In: *bioRxiv* (22nd Dec. 2020), p. 2020.12.08.413955. DOI: [10.1101/2020.12.08.413955](https://doi.org/10.1101/2020.12.08.413955).
- [124] M. Ilius, R. Wolf and M. Heisenberg. “The Central Complex of *Drosophila Melanogaster* Is Involved in Flight Control: Studies on Mutants and Mosaics of the Gene *Ellipsoid Body Open*”. In: *Journal of Neurogenetics* 21.4 (1st Jan. 2007), pp. 321–338. ISSN: 0167-7063. DOI: [10.1080/01677060701693503](https://doi.org/10.1080/01677060701693503).
- [125] A. C. James. “Nonlinear Operator Network Models of Processing in the Fly Lamina”. In: *Nonlinear Vision: Determination of Neural Receptive Fields, Function, and Networks*. CRC Press, 1992. ISBN: 978-1-351-07506-0.
- [126] Piyankarie Jayatilaka et al. “The Choreography of Learning Walks in the Australian Jack Jumper Ant *Myrmecia Croslandi*”. In: *The Journal of Experimental Biology* 221.20 (15th Oct. 2018), jeb185306. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/JEB.185306](https://doi.org/10.1242/JEB.185306).

-
- [127] Ron A. Jortner, S. Sarah Farivar and Gilles Laurent. “A Simple Connectivity Scheme for Sparse Coding in an Olfactory System”. In: *Journal of Neuroscience* 27.7 (14th Feb. 2007), pp. 1659–1669. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.4171-06.2007](https://doi.org/10.1523/JNEUROSCI.4171-06.2007).
- [128] J. Frances Kamhi, Andrew B. Barron and Ajay Narendra. “Vertical Lobes of the Mushroom Bodies Are Essential for View-Based Navigation in Australian Myrmecia Ants”. In: *Current Biology* 30.17 (7th Sept. 2020), 3432–3437.e3. ISSN: 0960-9822. DOI: [10.1016/j.cub.2020.06.030](https://doi.org/10.1016/j.cub.2020.06.030).
- [129] R. Kanzaki and T. Shibuya. “Long-Lasting Excitation of Protocerebral Bilateral Neurons in the Pheromone-Processing Pathways of the Male Moth *Bombyx Mori*”. In: *Brain Research* 587.2 (7th Aug. 1992), pp. 211–215. ISSN: 0006-8993. DOI: [10.1016/0006-8993\(92\)90999-p](https://doi.org/10.1016/0006-8993(92)90999-p).
- [130] N. D. Kathman, M. Kesavan and R. E. Ritzmann. “Encoding Wide-Field Motion and Direction in the Central Complex of the Cockroach *Blaberus Discoidalis*”. In: *Journal of Experimental Biology* 217.22 (15th Nov. 2014), pp. 4079–4090. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.112391](https://doi.org/10.1242/jeb.112391).
- [131] F. C. Kenyon. “The Brain of the Bee. A Preliminary Contribution to the Morphology of the Nervous System of the Arthropoda”. In: *Journal of Comparative Neurology* 6.3 (Mar. 1896), pp. 133–210. ISSN: 0092-7317, 1550-7130. DOI: [10.1002/cne.910060302](https://doi.org/10.1002/cne.910060302).
- [132] DaeEun Kim and John C. T. Hallam. “Neural Network Approach to Path Integration for Homing Navigation”. In: *From Animals to Animats 6*. MIT press, 2000, pp. 228–235. ISBN: 978-0-262-31607-1. URL: https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_724836 (visited on 02/03/2020).
- [133] Irene S Kim and Michael H Dickinson. “Idiothetic Path Integration in the Fruit Fly *Drosophila Melanogaster*”. In: *Current Biology* 27.15 (2017), pp. 2227–2238. DOI: [10.1016/j.cub.2017.06.026](https://doi.org/10.1016/j.cub.2017.06.026).
- [134] Sung Soo Kim et al. “Generation of Stable Heading Representations in Diverse Visual Scenes”. In: *Nature* 576.7785 (Dec. 2019), pp. 126–131. ISSN: 0028-0836, 1476-4687. DOI: [10.1038/s41586-019-1767-1](https://doi.org/10.1038/s41586-019-1767-1).
- [135] Sung Soo Kim et al. “Ring Attractor Dynamics in the *Drosophila* Central Brain”. In: *Science* 356.6340 (26th May 2017), pp. 849–853. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.aal4835](https://doi.org/10.1126/science.aal4835).
- [136] K. Kirschfeld. “The Resolution of Lens and Compound Eyes”. In: *Neural Principles in Vision*. Ed. by Friedrich Zettler and Reto Weiler. Proceedings in Life Sciences. Springer Berlin Heidelberg, 1976, pp. 354–370. ISBN: 978-3-642-66432-8.

- [137] Markus Knaden and Paul Graham. “The Sensory Ecology of Ant Navigation: From Natural Environments to Neural Mechanisms”. In: *Annual Review of Entomology* 61.1 (2016), pp. 63–76. DOI: [10.1146/annurev-ento-010715-023703](https://doi.org/10.1146/annurev-ento-010715-023703).
- [138] Markus Knaden and Rüdiger Wehner. “Path Integration in Desert Ants Controls Aggressiveness”. In: *Science* 305.5680 (2nd July 2004), pp. 60–60. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.1097165](https://doi.org/10.1126/science.1097165).
- [139] Aleksandar Kodzhabashev and Michael Mangan. “Route Following Without Scanning”. In: *Biomimetic and Biohybrid Systems*. Ed. by Stuart P. Wilson et al. Vol. 9222. Cham: Springer International Publishing, 2015, pp. 199–210. ISBN: 978-3-319-22978-2 978-3-319-22979-9. DOI: [10.1007/978-3-319-22979-9_20](https://doi.org/10.1007/978-3-319-22979-9_20).
- [140] Martin Kohler and Rüdiger Wehner. “Idiosyncratic Route-Based Memories in Desert Ants, *Melophorus Bagoti*: How Do They Interact with Path-Integration Vectors?” In: *Neurobiology of Learning and Memory* 83.1 (Jan. 2005), pp. 1–12. ISSN: 10747427. DOI: [10.1016/j.nlm.2004.05.011](https://doi.org/10.1016/j.nlm.2004.05.011).
- [141] Thomas Kollmeier et al. “Spectral Contrasts for Landmark Navigation”. In: *JOSA A* 24.1 (1st Jan. 2007), pp. 1–10. ISSN: 1520-8532. DOI: [10.1364/JOSAA.24.000001](https://doi.org/10.1364/JOSAA.24.000001).
- [142] Eric C Kong et al. “A Pair of Dopamine Neurons Target the D1-like Dopamine Receptor DopR in the Central Complex to Promote Ethanol-Stimulated Locomotion in *Drosophila*”. In: *PloS one* 5.4 (2010), e9954. DOI: [10.1371/journal.pone.0009954](https://doi.org/10.1371/journal.pone.0009954).
- [143] Simone Kühn-Bühlmann and Rüdiger Wehner. “Age-Dependent and Task-Related Volume Changes in the Mushroom Bodies of Visually Guided Desert Ants, *Cataglyphis Bicolor*”. In: *Journal of Neurobiology* 66.6 (May 2006), pp. 511–521. ISSN: 0022-3034. DOI: [10.1002/neu.20235](https://doi.org/10.1002/neu.20235).
- [144] Dimitrios Lambrinos et al. “An Autonomous Agent Navigating with a Polarized Light Compass”. In: *Adaptive Behavior* 6.1 (1st June 1997), pp. 131–161. ISSN: 1059-7123. DOI: [10.1177/105971239700600104](https://doi.org/10.1177/105971239700600104).
- [145] Michael F. Land. “Visual Acuity in Insects”. In: *Annual Review of Entomology* 42.1 (1997), pp. 147–177. DOI: [10.1146/annurev.ento.42.1.147](https://doi.org/10.1146/annurev.ento.42.1.147).
- [146] Gilles Laurent. “Olfactory Network Dynamics and the Coding of Multidimensional Signals”. In: *Nature Reviews Neuroscience* 3.11 (11 Nov. 2002), pp. 884–895. ISSN: 1471-0048. DOI: [10.1038/nrn964](https://doi.org/10.1038/nrn964).
- [147] Yu-Jen Lee, H. Olof Jönsson and Karin Nordström. “Spatio-Temporal Dynamics of Impulse Responses to Figure Motion in Optic Flow Neurons”. In: *PLOS ONE* 10.5 (8th May 2015), e0126265. ISSN: 1932-6203. DOI: [10.1371/journal.pone.0126265](https://doi.org/10.1371/journal.pone.0126265).

- [148] Eric LG Legge et al. “Combining Sky and Earth: Desert Ants (*Melophorus Bagoti*) Show Weighted Integration of Celestial and Terrestrial Cues”. In: *Journal of Experimental Biology* 217.23 (2014), pp. 4159–4166. DOI: [10.1242/jeb.107862](https://doi.org/10.1242/jeb.107862).
- [149] B. Leitch and G. Laurent. “GABAergic Synapses in the Antennal Lobe and Mushroom Body of the Locust Olfactory System”. In: *The Journal of Comparative Neurology* 372.4 (2nd Sept. 1996), pp. 487–514. ISSN: 0021-9967. DOI: [10.1002/\(SICI\)1096-9861\(19960902\)372:4<487::AID-CNE1>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1096-9861(19960902)372:4<487::AID-CNE1>3.0.CO;2-0).
- [150] David D. Lent, Paul Graham and Thomas S. Collett. “Visual Scene Perception in Navigating Wood Ants”. In: *Current Biology* 23.8 (22nd Apr. 2013), pp. 684–690. ISSN: 0960-9822. DOI: [10.1016/j.cub.2013.03.016](https://doi.org/10.1016/j.cub.2013.03.016).
- [151] Jinzhi Li et al. “Two Parallel Pathways Convey Distinct Visual Information to the Drosophila Mushroom Body”. In: *bioRxiv* (7th Feb. 2020), p. 2020.02.07.935924. DOI: [10.1101/2020.02.07.935924](https://doi.org/10.1101/2020.02.07.935924).
- [152] Xu Liu and Ronald L. Davis. “The GABAergic Anterior Paired Lateral Neuron Suppresses and Is Suppressed by Olfactory Learning”. In: *Nature Neuroscience* 12.1 (1 Jan. 2009), pp. 53–59. ISSN: 1546-1726. DOI: [10.1038/nn.2235](https://doi.org/10.1038/nn.2235).
- [153] Jenny Lu et al. “Transforming Representations of Movement from Body- to World-Centric Space”. In: *bioRxiv* (23rd Dec. 2020), p. 2020.12.22.424001. DOI: [10.1101/2020.12.22.424001](https://doi.org/10.1101/2020.12.22.424001).
- [154] Cheng Lyu, L. F. Abbott and Gaby Maimon. “A Neuronal Circuit for Vector Computation Builds an Allocentric Traveling-Direction Signal in the Drosophila Fan-Shaped Body”. In: *bioRxiv* (23rd Dec. 2020), p. 2020.12.22.423967. DOI: [10.1101/2020.12.22.423967](https://doi.org/10.1101/2020.12.22.423967).
- [155] Michael Mangan and Barbara Webb. “Spontaneous Formation of Multiple Routes in Individual Desert Ants (*Cataglyphis Velox*)”. In: *Behavioral Ecology* 23.5 (2012), pp. 944–954. ISSN: 1465-7279, 1045-2249. DOI: [10.1093/beheco/ars051](https://doi.org/10.1093/beheco/ars051).
- [156] S. Marčelja. “Optimal Lateral Interactions in a Compound Eye”. In: *Journal of comparative physiology* 132.2 (1979), pp. 159–166.
- [157] David Marr. “Vision: A Computational Investigation into the Human Representation and Processing of Visual Information, Henry Holt and Co”. In: *Inc., New York, NY* 2.4.2 (1982).
- [158] A. C. Marsh. “Microclimatic Factors Influencing Foraging Patterns and Success of the Thermophilic Desert Ant, *Ocymyrmex Barbiger*”. In: *Insectes Sociaux* 32.3 (1st Sept. 1985), pp. 286–296. ISSN: 1420-9098. DOI: [10.1007/BF02224917](https://doi.org/10.1007/BF02224917).
- [159] Joshua P. Martin et al. “Central-Complex Control of Movement in the Freely Walking Cockroach”. In: *Current Biology* 25.21 (Nov. 2015), pp. 2795–2803. ISSN: 09609822. DOI: [10.1016/J.CUB.2015.09.044](https://doi.org/10.1016/J.CUB.2015.09.044).

- [160] Krishna V. Melnattur and Chi-Hon Lee. “Visual Circuit Assembly in *Drosophila*”. In: *Developmental neurobiology* 71.12 (Dec. 2011), pp. 1286–1296. ISSN: 1932-8451. DOI: [10.1002/dneu.20894](https://doi.org/10.1002/dneu.20894).
- [161] R. Menzel et al. “Honey Bees Navigate According to a Map-like Spatial Memory”. In: *Proceedings of the National Academy of Sciences* 102.8 (22nd Feb. 2005), pp. 3040–3045. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.0408550102](https://doi.org/10.1073/pnas.0408550102).
- [162] Randolph Menzel. “The Insect Mushroom Body, an Experience-Dependent Recoding Device”. In: *Journal of Physiology, Paris* 108.2-3 (2014 Apr-Jun), pp. 84–95. ISSN: 1769-7115. DOI: [10.1016/j.jphysparis.2014.07.004](https://doi.org/10.1016/j.jphysparis.2014.07.004).
- [163] Randolph Menzel and Uwe Greggers. “The Memory Structure of Navigation in Honeybees”. In: *Journal of Comparative Physiology A* 201.6 (1st June 2015), pp. 547–561. ISSN: 1432-1351. DOI: [10.1007/s00359-015-0987-6](https://doi.org/10.1007/s00359-015-0987-6).
- [164] Tobias Merkle, Markus Knaden and Rüdiger Wehner. “Uncertainty about Nest Position Influences Systematic Search Strategies in Desert Ants”. In: *Journal of Experimental Biology* 209.18 (15th Sept. 2006), pp. 3545–3549. ISSN: 0022-0949. DOI: [10.1242/jeb.02395](https://doi.org/10.1242/jeb.02395).
- [165] Tobias Merkle and Rüdiger Wehner. “Desert Ants Use Foraging Distance to Adapt the Nest Search to the Uncertainty of the Path Integrator”. In: *Behavioral Ecology* 21.2 (1st Mar. 2010), pp. 349–355. ISSN: 1045-2249. DOI: [10.1093/beheco/arp197](https://doi.org/10.1093/beheco/arp197).
- [166] Tobias Merkle and Rüdiger Wehner. “How Flexible Is the Systematic Search Behaviour of Desert Ants?” In: *Animal Behaviour* 77.5 (2009), pp. 1051–1056. DOI: [10.1016/j.anbehav.2009.01.006](https://doi.org/10.1016/j.anbehav.2009.01.006).
- [167] Hedi W. Meyer. “Visuelle Schlüsselreize für die Auslösung der Beutefanghandlung beim Bachwasserläufer *Velia caprai* (Hemiptera, Heteroptera)”. In: *Zeitschrift für vergleichende Physiologie* 72.3 (1st Sept. 1971), pp. 298–342. ISSN: 1432-1351. DOI: [10.1007/BF00297784](https://doi.org/10.1007/BF00297784).
- [168] Michael Milford. “Vision-Based Place Recognition: How Low Can You Go?” In: *The International Journal of Robotics Research* 32.7 (June 2013), pp. 766–789. ISSN: 0278-3649, 1741-3176. DOI: [10.1177/0278364913490323](https://doi.org/10.1177/0278364913490323).
- [169] T. Mishima and R. Kanzaki. “Physiological and Morphological Characterization of Olfactory Descending Interneurons of the Male Silkworm Moth, *Bombyx Mori*”. In: *Journal of Comparative Physiology A* 184.2 (1st Mar. 1999), pp. 143–160. ISSN: 1432-1351. DOI: [10.1007/s003590050314](https://doi.org/10.1007/s003590050314).
- [170] H. Mittelstaedt and M.-L. Mittelstaedt. “Homing by Path Integration”. In: *Avian Navigation*. Ed. by Floriano Papi and Hans G. Wallraff. Proceedings in Life Sciences. Berlin, Heidelberg: Springer, 1982, pp. 290–297. ISBN: 978-3-642-68616-0. DOI: [10.1007/978-3-642-68616-0_29](https://doi.org/10.1007/978-3-642-68616-0_29).

- [171] Horst Mittelstaedt and Marie Luise Mittelstaedt. “Mechanismen Der Orientierung Ohne Richtende Außenreize”. In: First International Symposium of the Academy of Sciences and Literature. Gustav Fischer Verlag, 1973, pp. 46–58. URL: https://pure.mpg.de/pubman/faces/ViewItemFullPage.jsp?itemId=item_2250818_5 (visited on 07/06/2021).
- [172] M. Mizunami, J. M. Weibrecht and N. J. Strausfeld. “Mushroom Bodies of the Cockroach: Their Participation in Place Memory”. In: *The Journal of Comparative Neurology* 402.4 (28th Dec. 1998), pp. 520–537. ISSN: 0021-9967.
- [173] P. G. Mobbs. “Neural Networks in the Mushroom Bodies of the Honeybee”. In: *Journal of Insect Physiology* 30.1 (1st Jan. 1984), pp. 43–58. ISSN: 0022-1910. DOI: [10.1016/0022-1910\(84\)90107-0](https://doi.org/10.1016/0022-1910(84)90107-0).
- [174] P. G. Mobbs and John Zachary Young. “The Brain of the Honeybee *Apis Mellifera*. I. The Connections and Spatial Organization of the Mushroom Bodies”. In: *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 298.1091 (27th July 1982), pp. 309–354. DOI: [10.1098/rstb.1982.0086](https://doi.org/10.1098/rstb.1982.0086).
- [175] Mehrab N. Modi, Yichun Shuai and Glenn C. Turner. “The *Drosophila* Mushroom Body: From Architecture to Algorithm in a Learning Circuit”. In: *Annual Review of Neuroscience* (13th Apr. 2020). ISSN: 1545-4126. DOI: [10.1146/annurev-neuro-080317-0621333](https://doi.org/10.1146/annurev-neuro-080317-0621333).
- [176] Ralf Möller. “Do Insects Use Templates or Parameters for Landmark Navigation?” In: *Journal of Theoretical Biology* 210.1 (7th May 2001), pp. 33–45. ISSN: 0022-5193. DOI: [10.1006/jtbi.2001.2295](https://doi.org/10.1006/jtbi.2001.2295).
- [177] Ralf Möller. “Insects Could Exploit UV–Green Contrast for Landmark Navigation”. In: *Journal of Theoretical Biology* 214.4 (Feb. 2002), pp. 619–631. ISSN: 00225193. DOI: [10.1006/jtbi.2001.2484](https://doi.org/10.1006/jtbi.2001.2484).
- [178] Ralf Möller and Andrew Vardy. “Local Visual Homing by Matched-Filter Descent in Image Distances”. In: *Biological Cybernetics* 95.5 (1st Nov. 2006), pp. 413–430. ISSN: 1432-0770. DOI: [10.1007/s00422-006-0095-3](https://doi.org/10.1007/s00422-006-0095-3).
- [179] Ralf Möller et al. “Modeling Ant Navigation with an Autonomous Agent”. In: *In Proc. 5th Int. Conf. Simulation of Adaptive Behavior*. MIT Press, 1998, pp. 185–194.
- [180] Javier Morante, Claude Desplan and Arzu Celik. “Generating Patterned Arrays of Photoreceptors”. In: *Current Opinion in Genetics & Development*. Pattern Formation and Developmental Mechanisms 17.4 (1st Aug. 2007), pp. 314–319. ISSN: 0959-437X. DOI: [10.1016/j.gde.2007.05.003](https://doi.org/10.1016/j.gde.2007.05.003).
- [181] Corrie S. Moreau et al. “Phylogeny of the Ants: Diversification in the Age of Angiosperms”. In: *Science* 312.5770 (7th Apr. 2006), pp. 101–104. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.1124891](https://doi.org/10.1126/science.1124891).

- [182] Michael I. Mote and Rüdiger Wehner. “Functional Characteristics of Photoreceptors in the Compound Eye and Ocellus of the Desert Ant, *Cataglyphis Bicolor*”. In: *Journal of Comparative Physiology ? A* 137.1 (1980), pp. 63–71. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/BF00656918](https://doi.org/10.1007/BF00656918).
- [183] Henrik Mouritsen et al. “An Experimental Displacement and over 50 Years of Tag-Recoveries Show That Monarch Butterflies Are Not True Navigators”. In: *Proceedings of the National Academy of Sciences* 110.18 (30th Apr. 2013), pp. 7348–7353. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.1221701110](https://doi.org/10.1073/pnas.1221701110).
- [184] Thomas S. Muenz et al. “Neuronal Plasticity in the Mushroom Body Calyx during Adult Maturation in the Honeybee and Possible Pheromonal Influences”. In: *Developmental Neurobiology* 75.12 (2015), pp. 1368–1384. ISSN: 1932-846X. DOI: [10.1002/dneu.22290](https://doi.org/10.1002/dneu.22290).
- [185] Jurek Müller et al. “A Neural Network Model for Familiarity and Context Learning during Honeybee Foraging Flights”. In: *Biological Cybernetics* 112.1 (1st Apr. 2018), pp. 113–126. ISSN: 1432-0770. DOI: [10.1007/s00422-017-0732-z](https://doi.org/10.1007/s00422-017-0732-z).
- [186] M. Müller and R. Wehner. “The Hidden Spiral: Systematic Search and Path Integration in Desert Ants, *Cataglyphis Fortis*”. In: *Journal of Comparative Physiology A* 175.5 (1st Nov. 1994), pp. 525–530. ISSN: 1432-1351. DOI: [10.1007/BF00199474](https://doi.org/10.1007/BF00199474).
- [187] Martin Müller and Rüdiger Wehner. “Path Integration Provides a Scaffold for Landmark Learning in Desert Ants”. In: *Current Biology* 20.15 (Aug. 2010), pp. 1368–1371. DOI: [10.1016/j.cub.2010.06.035](https://doi.org/10.1016/j.cub.2010.06.035).
- [188] Martin Müller and Rüdiger Wehner. “Wind and Sky as Compass Cues in Desert Ant Navigation”. In: *Naturwissenschaften* 94.7 (1st July 2007), pp. 589–594. ISSN: 1432-1904. DOI: [10.1007/s00114-007-0232-4](https://doi.org/10.1007/s00114-007-0232-4).
- [189] Monika Müller, Uwe Homberg and Angelika Kühn. “Neuroarchitecture of the Lower Division of the Central Body in the Brain of the Locust (*Schistocerca Gregaria*)”. In: *Cell and Tissue Research* 288.1 (1st Mar. 1997), pp. 159–176. ISSN: 1432-0878. DOI: [10.1007/s004410050803](https://doi.org/10.1007/s004410050803).
- [190] Trevor Murray and Jochen Zeil. “Quantifying Navigational Information: The Catchment Volumes of Panoramic Snapshots in Outdoor Scenes”. In: *PLOS ONE* 12.10 (31st Oct. 2017). Ed. by Paul Graham, e0187226. ISSN: 1932-6203. DOI: [10.1371/JOURNAL.PONE.0187226](https://doi.org/10.1371/JOURNAL.PONE.0187226).
- [191] Trevor Murray et al. “The Role of Attractive and Repellent Scene Memories in Ant Homing (*Myrmecia Croslandi*)”. In: *Journal of Experimental Biology* 223.3 (1st Feb. 2020). ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.210021](https://doi.org/10.1242/jeb.210021).
- [192] Barbara Muser et al. “Foraging Ecology of the Thermophilic Australian Desert Ant, *Melophorus Bagoti*”. In: *Australian Journal of Zoology* 53.5 (2005), p. 301. ISSN: 0004-959X. DOI: [10.1071/ZO05023](https://doi.org/10.1071/ZO05023).

-
- [193] Shigehiro Namiki and Ryohei Kanzaki. “The Neurobiological Basis of Orientation in Insects: Insights from the Silkmother Mating Dance”. In: *Current Opinion in Insect Science*. Pests and Resistance * Behavioural Ecology 15 (1st June 2016), pp. 16–26. ISSN: 2214-5745. DOI: [10.1016/j.cois.2016.02.009](https://doi.org/10.1016/j.cois.2016.02.009).
- [194] Shigehiro Namiki, Satoshi Wada and Ryohei Kanzaki. “Descending Neurons from the Lateral Accessory Lobe and Posterior Slope in the Brain of the Silkmother Bombyx Mori”. In: *Scientific Reports* 8.1 (1 25th June 2018), p. 9663. ISSN: 2045-2322. DOI: [10.1038/s41598-018-27954-5](https://doi.org/10.1038/s41598-018-27954-5).
- [195] Shigehiro Namiki et al. “Information Flow through Neural Circuits for Pheromone Orientation”. In: *Nature Communications* 5.1 (1 23rd Dec. 2014), p. 5919. ISSN: 2041-1723. DOI: [10.1038/ncomms6919](https://doi.org/10.1038/ncomms6919).
- [196] Ajay Narendra, Sarah Gourmaud and Jochen Zeil. “Mapping the Navigational Knowledge of Individually Foraging Ants, *Myrmecia Croslandi*”. In: *Proceedings. Biological Sciences* 280.1765 (22nd Aug. 2013), p. 20130683. ISSN: 1471-2954. DOI: [10.1098/rspb.2013.0683](https://doi.org/10.1098/rspb.2013.0683).
- [197] Ajay Narendra et al. “Search Strategies of Ants in Landmark-Rich Habitats”. In: *Journal of Comparative Physiology A* 194.11 (1st Nov. 2008), pp. 929–938. ISSN: 1432-1351. DOI: [10.1007/s00359-008-0365-8](https://doi.org/10.1007/s00359-008-0365-8).
- [198] Titus R. Neumann. “Modeling Insect Compound Eyes: Space-Variant Spherical Vision”. In: *Biologically Motivated Computer Vision*. Ed. by Heinrich H. Bülthoff et al. Lecture Notes in Computer Science. Berlin, Heidelberg: Springer, 2002, pp. 360–367. ISBN: 978-3-540-36181-7. DOI: [10.1007/3-540-36181-2_36](https://doi.org/10.1007/3-540-36181-2_36).
- [199] D. J. Nicholson et al. “Learning Walks and Landmark Guidance in Wood Ants (*Formica Rufa*)”. In: *The Journal of Experimental Biology* 202 (Pt 13) (July 1999), pp. 1831–1838. ISSN: 1477-9145.
- [200] Thomas Nowotny et al. “Decoding Temporal Information through Slow Lateral Excitation in the Olfactory System of Insects”. In: *Journal of Computational Neuroscience* 15.2 (2003 Sep-Oct), pp. 271–281. ISSN: 0929-5313. DOI: [10.1023/A:1025825111088](https://doi.org/10.1023/A:1025825111088).
- [201] Tatsuo S. Okubo et al. “A Neural Network for Wind-Guided Compass Navigation”. In: *Neuron* 107.5 (9th Sept. 2020), 924–940.e18. ISSN: 1097-4199. DOI: [10.1016/j.neuron.2020.06.022](https://doi.org/10.1016/j.neuron.2020.06.022).
- [202] David Oswald and Scott Waddell. “Olfactory Learning Skews Mushroom Body Output Pathways to Steer Behavioral Choice in *Drosophila*”. In: *Current Opinion in Neurobiology*. Circuit Plasticity and Memory 35 (1st Dec. 2015), pp. 178–184. ISSN: 0959-4388. DOI: [10.1016/j.conb.2015.10.002](https://doi.org/10.1016/j.conb.2015.10.002).

- [203] Rickesh N. Patel and Thomas W. Cronin. “Mantis Shrimp Navigate Home Using Celestial and Idiothetic Path Integration”. In: *Current Biology* 30.11 (8th June 2020), 1981–1987.e3. ISSN: 0960-9822. DOI: [10.1016/j.cub.2020.03.023](https://doi.org/10.1016/j.cub.2020.03.023).
- [204] Angelique C. Paulk et al. “Closed-Loop Behavioral Control Increases Coherence in the Fly Brain”. In: *Journal of Neuroscience* 35.28 (15th July 2015), pp. 10304–10315. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.0691-15.2015](https://doi.org/10.1523/JNEUROSCI.0691-15.2015).
- [205] Angelique C. Paulk et al. “Visual Processing in the Central Bee Brain”. In: *Journal of Neuroscience* 29.32 (12th Aug. 2009), pp. 9987–9999. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.1325-09.2009](https://doi.org/10.1523/JNEUROSCI.1325-09.2009).
- [206] Uta Pegel et al. “Two Compasses in the Central Complex of the Locust Brain”. In: *Journal of Neuroscience* 39.16 (17th Apr. 2019), pp. 3070–3080. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.0940-18.2019](https://doi.org/10.1523/JNEUROSCI.0940-18.2019).
- [207] J. Perez-Orive. “Oscillations and Sparsening of Odor Representations in the Mushroom Body”. In: *Science* 297.5580 (19th July 2002), pp. 359–365. ISSN: 00368075, 10959203. DOI: [10.1126/science.1070502](https://doi.org/10.1126/science.1070502).
- [208] Emmanuel Perisse et al. “Aversive Learning and Appetitive Motivation Toggle Feed-Forward Inhibition in the Drosophila Mushroom Body”. In: *Neuron* 90.5 (June 2016), pp. 1086–1099. ISSN: 08966273. DOI: [10.1016/j.neuron.2016.04.034](https://doi.org/10.1016/j.neuron.2016.04.034).
- [209] Sarah Pfeffer and Harald Wolf. “Arthropod Spatial Cognition”. In: *Animal Cognition* 23.6 (1st Nov. 2020), pp. 1041–1049. ISSN: 1435-9456. DOI: [10.1007/s10071-020-01446-4](https://doi.org/10.1007/s10071-020-01446-4).
- [210] Sarah Elisabeth Pfeffer et al. “High-Speed Locomotion in the Saharan Silver Ant, *Cataglyphis bombycina*”. In: *The Journal of Experimental Biology* 222.20 (15th Oct. 2019), jeb198705. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.198705](https://doi.org/10.1242/jeb.198705).
- [211] Keram Pfeiffer and Uwe Homberg. “Organization and Functional Roles of the Central Complex in the Insect Brain”. In: *Annual Review of Entomology* 59.1 (7th Jan. 2014), pp. 165–184. ISSN: 0066-4170. DOI: [10.1146/annurev-ento-011613-162031](https://doi.org/10.1146/annurev-ento-011613-162031).
- [212] Andrew Philippides et al. “How Active Vision Facilitates Familiarity-Based Homing”. In: *Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*. Vol. 8064 LNAI. 2013, pp. 427–430. ISBN: 978-3-642-39801-8. DOI: [10.1007/978-3-642-39802-5-56](https://doi.org/10.1007/978-3-642-39802-5-56).
- [213] Andrew Philippides et al. “How Might Ants Use Panoramic Views for Route Navigation?” In: *Journal of Experimental Biology* 214.3 (1st Feb. 2011), pp. 445–451. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.046755](https://doi.org/10.1242/jeb.046755).

-
- [214] H. Pieron. “Du Role Du Sens Musculaire Dans l’orientation de Quelques Espèces de Fourmis”. In: *Bull. Inst. Gen. Psychol* 4 (1904), pp. 168–186.
- [215] Maxwell E. Power. “The Brain of *Drosophila Melanogaster*”. In: *Journal of Morphology* 72.3 (1943), pp. 517–559. ISSN: 1097-4687. DOI: [10.1002/jmor.1050720306](https://doi.org/10.1002/jmor.1050720306).
- [216] Aleksandr Rayshubskiy et al. “Neural Control of Steering in Walking *Drosophila*”. In: *bioRxiv* (5th Apr. 2020), p. 2020.04.04.024703. DOI: [10.1101/2020.04.04.024703](https://doi.org/10.1101/2020.04.04.024703).
- [217] S. F. Reid et al. “Polarised Skylight and the Landmark Panorama Provide Night-Active Bull Ants with Compass Information during Route Following”. In: *Journal of Experimental Biology* 214.3 (1st Feb. 2011), pp. 363–370. ISSN: 0022-0949, 1477-9145. DOI: [10.1242/jeb.049338](https://doi.org/10.1242/jeb.049338).
- [218] Andrew M. Reynolds et al. “Displaced Honey Bees Perform Optimal Scale-Free Search Flights”. In: *Ecology* 88.8 (2007), pp. 1955–1961. ISSN: 0012-9658. JSTOR: [27651326](https://www.jstor.org/stable/27651326).
- [219] C. R. Ribbands. “The Foraging Method of Individual Honey-Bees”. In: *Journal of Animal Ecology* 18.1 (1949), pp. 47–66. ISSN: 0021-8790. DOI: [10.2307/1581](https://doi.org/10.2307/1581). JSTOR: [1581](https://www.jstor.org/stable/1581).
- [220] W. A. Ribi. “Golgi Studies of the First Optic Ganglion of the Ant, *Cataglyphis Bicolor*”. In: *Cell and Tissue Research* 160.2 (8th July 1975), pp. 207–217. ISSN: 0302-766X. DOI: [10.1007/BF00220578](https://doi.org/10.1007/BF00220578).
- [221] W. A. Ribi. “Neurons in the First Synaptic Region of the Bee, *Apis Mellifera*”. In: *Cell and Tissue Research* 148.2 (11th Apr. 1974), pp. 277–286. ISSN: 0302-766X. DOI: [10.1007/BF00224588](https://doi.org/10.1007/BF00224588).
- [222] Willi A. Ribi. “The First Optic Ganglion of the Bee”. In: *Cell and Tissue Research* 165.1 (1st Dec. 1975), pp. 103–111. ISSN: 1432-0878. DOI: [10.1007/BF00222803](https://doi.org/10.1007/BF00222803).
- [223] Angela L. Ridgel, Blythe E. Alexander and Roy E. Ritzmann. “Descending Control of Turning Behavior in the Cockroach, *Blaberus Discoidalis*”. In: *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 193.4 (Apr. 2007), pp. 385–402. ISSN: 0340-7594. DOI: [10.1007/s00359-006-0193-7](https://doi.org/10.1007/s00359-006-0193-7).
- [224] J. R. Riley et al. “The Flight Paths of Honeybees Recruited by the Waggle Dance”. In: *Nature* 435.7039 (7039 May 2005), pp. 205–207. ISSN: 1476-4687. DOI: [10.1038/nature03526](https://doi.org/10.1038/nature03526).
- [225] JR Riley et al. “Compensation for Wind Drift by Bumble-Bees”. In: *Nature* 400.6740 (1999), p. 126. DOI: [10.1038/22029](https://doi.org/10.1038/22029).

- [226] Benjamin Risse et al. “Software to Convert Terrestrial LiDAR Scans of Natural Environments into Photorealistic Meshes”. In: *Environmental modelling & software* 99 (2018), pp. 88–100. DOI: [10.1016/j.envsoft.2017.09.018](https://doi.org/10.1016/j.envsoft.2017.09.018).
- [227] Roy E. Ritzmann, Angela L. Ridgel and Alan J. Pollack. “Multi-Unit Recording of Antennal Mechano-Sensitive Units in the Central Complex of the Cockroach, *Blaberus Discoidalis*”. In: *Journal of Comparative Physiology A* 194.4 (Apr. 2008), pp. 341–360. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/s00359-007-0310-2](https://doi.org/10.1007/s00359-007-0310-2).
- [228] Roy E. Ritzmann et al. “Deciding Which Way to Go: How Do Insects Alter Movements to Negotiate Barriers?” In: *Frontiers in Neuroscience* 6 (2012), p. 97. ISSN: 1662-453X. DOI: [10.3389/fnins.2012.00097](https://doi.org/10.3389/fnins.2012.00097).
- [229] B. Ronacher and R. Wehner. “Desert Ants *Cataglyphis Fortis* Use Self-Induced Optic Flow to Measure Distances Travelled”. In: *Journal of Comparative Physiology A* 177.1 (1st July 1995), pp. 21–27. ISSN: 1432-1351. DOI: [10.1007/BF00243395](https://doi.org/10.1007/BF00243395).
- [230] Ronny Rosner and Uwe Homberg. “Widespread Sensitivity to Looming Stimuli and Small Moving Objects in the Central Complex of an Insect Brain”. In: *Journal of Neuroscience* 33.19 (8th May 2013), pp. 8122–8133. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.5390-12.2013](https://doi.org/10.1523/JNEUROSCI.5390-12.2013).
- [231] Samuel Rossel and Rüdiger Wehner. “Celestial Orientation in Bees: The Use of Spectral Cues”. In: *Journal of Comparative Physiology A* 155.5 (1st Sept. 1984), pp. 605–613. ISSN: 1432-1351. DOI: [10.1007/BF00610846](https://doi.org/10.1007/BF00610846).
- [232] Wolfgang Rössler. “Neuroplasticity in Desert Ants (Hymenoptera: Formicidae) – Importance for the Ontogeny of Navigation”. In: *Myrmecological News* 29.0 (0 9th Jan. 2019). ISSN: 1997-3500. URL: <https://www.biotaxa.org/mn/article/view/44441> (visited on 02/05/2021).
- [233] Wolfgang Rössler and Claudia Groh. “Plasticity of Synaptic Microcircuits in the Mushroom-Body Calyx of the Honey Bee”. In: *Honeybee Neurobiology and Behavior: A Tribute to Randolph Menzel*. Ed. by C. Giovanni Galizia, Dorothea Eisenhardt and Martin Giurfa. Dordrecht: Springer Netherlands, 2012, pp. 141–153. ISBN: 978-94-007-2099-2. DOI: [10.1007/978-94-007-2099-2_12](https://doi.org/10.1007/978-94-007-2099-2_12).
- [234] Jürgen Rybak and R. Menzel. “Anatomy of the Mushroom Bodies in the Honey Bee Brain: The Neuronal Connections of the Alpha-Lobe”. In: *Journal of Comparative Neurology* 334.3 (1993), pp. 444–465. ISSN: 1096-9861. DOI: [10.1002/cne.903340309](https://doi.org/10.1002/cne.903340309).
- [235] Gilbert Ryle. *The Concept of Mind*. Senior Series. London, New York: Hutchinson’s University Library, 1949. 334 pp. ISBN: 978-0-09-023892-7.
- [236] Felix Santschi. “Observations et remarques critiques sur le mécanisme de l’orientation chez les fourmis.” In: *Revue suisse de zoologie*. t.19 (1911) (1911), pp. 303–336. URL: <https://www.biodiversitylibrary.org/item/40644>.

-
- [237] Marcel E. Sayre et al. “A Projectome of the Bumblebee Central Complex”. In: *bioRxiv* (29th Mar. 2021), p. 2021.03.26.437137. DOI: [10.1101/2021.03.26.437137](https://doi.org/10.1101/2021.03.26.437137).
- [238] Paul Schmid-Hempel and Regula Schmid-Hempel. “Life Duration and Turnover of Foragers in the Ant *Cataglyphis Bicolor* (Hymenoptera, Formicidae)”. In: *Insectes sociaux* 31.4 (1984), pp. 345–360.
- [239] Christopher Schnaitmann et al. “Color Discrimination with Broadband Photoreceptors”. In: *Current Biology* 23.23 (2nd Dec. 2013), pp. 2375–2382. ISSN: 0960-9822. DOI: [10.1016/j.cub.2013.10.037](https://doi.org/10.1016/j.cub.2013.10.037).
- [240] Christina Scholl et al. “Light Exposure Leads to Reorganization of Microglomeruli in the Mushroom Bodies and Influences Juvenile Hormone Levels in the Honeybee”. In: *Developmental Neurobiology* 74.11 (2014), pp. 1141–1153. ISSN: 1932-846X. DOI: [10.1002/dneu.22195](https://doi.org/10.1002/dneu.22195).
- [241] Timothy Duane Schowalter. *Insect Ecology: An Ecosystem Approach*. 4th edition. Amsterdam San Diego: Elsevier, 2016. 762 pp. ISBN: 978-0-12-803033-2.
- [242] Patrick Schultheiss and Ken Cheng. “Finding Food: Outbound Searching Behavior in the Australian Desert Ant *Melophorus Bagoti*”. In: *Behavioral Ecology* 24.1 (1st Jan. 2013), pp. 128–135. ISSN: 1045-2249. DOI: [10.1093/beheco/ars143](https://doi.org/10.1093/beheco/ars143).
- [243] Patrick Schultheiss and Ken Cheng. “Finding the Nest: Inbound Searching Behaviour in the Australian Desert Ant, *Melophorus Bagoti*”. In: *Animal Behaviour* 81.5 (1st May 2011), pp. 1031–1038. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2011.02.008](https://doi.org/10.1016/j.anbehav.2011.02.008).
- [244] Patrick Schultheiss, Ken Cheng and Andy M. Reynolds. “Searching Behavior in Social Hymenoptera”. In: *Learning and Motivation. Bee and Insect Learning and Cognition* 50 (1st May 2015), pp. 59–67. ISSN: 0023-9690. DOI: [10.1016/j.lmot.2014.11.002](https://doi.org/10.1016/j.lmot.2014.11.002).
- [245] Patrick Schultheiss et al. “Crucial Role of Ultraviolet Light for Desert Ants in Determining Direction from the Terrestrial Panorama”. In: *Animal Behaviour* 115 (2016), pp. 19–28. DOI: [10.1016/j.anbehav.2016.02.027](https://doi.org/10.1016/j.anbehav.2016.02.027).
- [246] Patrick Schultheiss et al. “Information Content of Visual Scenes Influences Systematic Search of Desert Ants”. In: *Journal of Experimental Biology* 216.4 (2013), pp. 742–749. DOI: [10.1242/jeb.075077](https://doi.org/10.1242/jeb.075077).
- [247] Ted R. Schultz. “In Search of Ant Ancestors”. In: *Proceedings of the National Academy of Sciences* 97.26 (19th Dec. 2000), pp. 14028–14029. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.011513798](https://doi.org/10.1073/pnas.011513798).

- [248] S. Schwarz et al. “Desert Ants (*Melophorus Bagoti*) Navigating with Robustness to Distortions of the Natural Panorama”. In: *Insectes Sociaux* 61.4 (Nov. 2014), pp. 371–383. ISSN: 0020-1812, 1420-9098. DOI: [10.1007/s00040-014-0364-4](https://doi.org/10.1007/s00040-014-0364-4).
- [249] Sebastian Schwarz, Ajay Narendra and Jochen Zeil. “The Properties of the Visual System in the Australian Desert Ant *Melophorus Bagoti*”. In: *Arthropod Structure & Development* 40.2 (1st Mar. 2011), pp. 128–134. ISSN: 1467-8039. DOI: [10.1016/j.asd.2010.10.003](https://doi.org/10.1016/j.asd.2010.10.003).
- [250] Sebastian Schwarz et al. “How Ants Use Vision When Homing Backward”. In: *Current Biology* 27.3 (Feb. 2017), pp. 401–407. DOI: [10.1016/j.cub.2016.12.019](https://doi.org/10.1016/j.cub.2016.12.019).
- [251] Sebastian Schwarz et al. “How Do Backward-Walking Ants (*Cataglyphis Velox*) Cope with Navigational Uncertainty?” In: *Animal Behaviour* 164 (1st June 2020), pp. 133–142. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2020.04.006](https://doi.org/10.1016/j.anbehav.2020.04.006).
- [252] Sebastian Schwarz et al. “Route-Following Ants Respond to Alterations of the View Sequence”. In: *The Journal of Experimental Biology* (2nd June 2020). ISSN: 1477-9145. DOI: [10.1242/jeb.218701](https://doi.org/10.1242/jeb.218701).
- [253] Johannes D. Seelig and Vivek Jayaraman. “Feature Detection and Orientation Tuning in the *Drosophila* Central Complex”. In: *Nature* 503.7475 (14th Nov. 2013), pp. 262–266. ISSN: 1476-4687. DOI: [10.1038/nature12601](https://doi.org/10.1038/nature12601).
- [254] Johannes D. Seelig and Vivek Jayaraman. “Neural Dynamics for Landmark Orientation and Angular Path Integration”. In: *Nature* 521.7551 (May 2015), pp. 186–191. ISSN: 1476-4687. DOI: [10.1038/nature14446](https://doi.org/10.1038/nature14446).
- [255] Marc A. Seid and Rüdiger Wehner. “Delayed Axonal Pruning in the Ant Brain: A Study of Developmental Trajectories”. In: *Developmental Neurobiology* 69.6 (2009), pp. 350–364. ISSN: 1932-846X. DOI: [10.1002/dneu.20709](https://doi.org/10.1002/dneu.20709).
- [256] Chi-Tin Shih et al. “Connectomics-Based Analysis of Information Flow in the *Drosophila* Brain”. In: *Current biology: CB* 25.10 (18th May 2015), pp. 1249–1258. ISSN: 1879-0445. DOI: [10.1016/j.cub.2015.03.021](https://doi.org/10.1016/j.cub.2015.03.021).
- [257] Allan W. Snyder, Doekele G. Stavenga and Simon B. Laughlin. “Spatial Information Capacity of Compound Eyes”. In: *Journal of Comparative Physiology ? A* 116.2 (1977), pp. 183–207. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/BF00605402](https://doi.org/10.1007/BF00605402).
- [258] Cwyn Solvi, Selene Gutierrez Al-Khudhairy and Lars Chittka. “Bumble Bees Display Cross-Modal Object Recognition between Visual and Tactile Senses”. In: *Science* 367.6480 (21st Feb. 2020), pp. 910–912. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.aay8064](https://doi.org/10.1126/science.aay8064).

-
- [259] Stefan Sommer and Rüdiger Wehner. “Leg Allometry in Ants: Extreme Long-Leggedness in Thermophilic Species”. In: *Arthropod Structure & Development* 41.1 (Jan. 2012), pp. 71–77. ISSN: 1873-5495. DOI: [10.1016/j.asd.2011.08.002](https://doi.org/10.1016/j.asd.2011.08.002).
- [260] Young Min Song et al. “Digital Cameras with Designs Inspired by the Arthropod Eye”. In: *Nature* 497.7447 (7447 May 2013), pp. 95–99. ISSN: 1476-4687. DOI: [10.1038/nature12083](https://doi.org/10.1038/nature12083).
- [261] M Srinivasan, S Zhang and N Bidwell. “Visually Mediated Odometry in Honeybees”. In: *Journal of Experimental Biology* 200.19 (1st Oct. 1997), pp. 2513–2522. ISSN: 0022-0949. DOI: [10.1242/jeb.200.19.2513](https://doi.org/10.1242/jeb.200.19.2513).
- [262] Mandyam Veerambudi Srinivasan et al. “Predictive Coding: A Fresh View of Inhibition in the Retina”. In: *Proceedings of the Royal Society of London. Series B. Biological Sciences* 216.1205 (22nd Nov. 1982), pp. 427–459. DOI: [10.1098/rspb.1982.0085](https://doi.org/10.1098/rspb.1982.0085).
- [263] Jan Stankiewicz and Barbara Webb. “Using the Neural Circuit of the Insect Central Complex for Path Integration on a Micro Aerial Vehicle”. In: *Biomimetic and Biohybrid Systems*. Ed. by Vasiliki Vouloutsi et al. Lecture Notes in Computer Science. Cham: Springer International Publishing, 2020, pp. 325–337. ISBN: 978-3-030-64313-3. DOI: [10.1007/978-3-030-64313-3_31](https://doi.org/10.1007/978-3-030-64313-3_31).
- [264] D. G. Stavenga. “Angular and Spectral Sensitivity of Fly Photoreceptors. I. Integrated Facet Lens and Rhabdomere Optics”. In: *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 189.1 (Jan. 2003), pp. 1–17. ISSN: 0340-7594. DOI: [10.1007/s00359-002-0370-2](https://doi.org/10.1007/s00359-002-0370-2).
- [265] D. G. Stavenga. “Angular and Spectral Sensitivity of Fly Photoreceptors. II. Dependence on Facet Lens F-Number and Rhabdomere Type in *Drosophila*”. In: *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 189.3 (Mar. 2003), pp. 189–202. ISSN: 0340-7594. DOI: [10.1007/s00359-003-0390-6](https://doi.org/10.1007/s00359-003-0390-6).
- [266] D. G. Stavenga. “Angular and Spectral Sensitivity of Fly Photoreceptors. III. Dependence on the Pupil Mechanism in the Blowfly *Calliphora*”. In: *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 190.2 (Feb. 2004), pp. 115–129. ISSN: 0340-7594. DOI: [10.1007/s00359-003-0477-0](https://doi.org/10.1007/s00359-003-0477-0).
- [267] Fabian Steinbeck, Andrea Adden and Paul Graham. “Connecting Brain to Behaviour: A Role for General Purpose Steering Circuits in Insect Orientation?” In: *The Journal of Experimental Biology* 223 (Pt 5 11th Mar. 2020). ISSN: 1477-9145. DOI: [10.1242/jeb.212332](https://doi.org/10.1242/jeb.212332).

- [268] Charles F. Stevens. “What the Fly’s Nose Tells the Fly’s Brain”. In: *Proceedings of the National Academy of Sciences of the United States of America* 112.30 (28th July 2015), pp. 9460–9465. ISSN: 0027-8424. DOI: [10.1073/pnas.1510103112](https://doi.org/10.1073/pnas.1510103112).
- [269] Sara Mae Stieb et al. “Visual Experience Affects Both Behavioral and Neuronal Aspects in the Individual Life History of the Desert Ant *Cataglyphis Fortis*”. In: *Developmental neurobiology* 72.5 (2012), pp. 729–742. DOI: [10.1002/dneu.20982](https://doi.org/10.1002/dneu.20982).
- [270] Sara Mae Stieb et al. “Visual Experience and Age Affect Synaptic Organization in the Mushroom Bodies of the Desert Ant *Cataglyphis Fortis*”. In: *Developmental Neurobiology* 70.6 (2010), pp. 408–423. ISSN: 1932-846X. DOI: [10.1002/dneu.20785](https://doi.org/10.1002/dneu.20785).
- [271] Thomas Stone et al. “An Anatomically Constrained Model for Path Integration in the Bee Brain”. In: *Current Biology* 27.20 (Oct. 2017), 3069–3085.e11. ISSN: 09609822. DOI: [10.1016/J.CUB.2017.08.052](https://doi.org/10.1016/J.CUB.2017.08.052).
- [272] Thomas Stone et al. “Rotation Invariant Visual Processing for Spatial Memory in Insects”. In: *Interface Focus* 8.4 (6th Aug. 2018), p. 20180010. DOI: [10.1098/rsfs.2018.0010](https://doi.org/10.1098/rsfs.2018.0010).
- [273] Thomas Stone et al. “Sky Segmentation with Ultraviolet Images Can Be Used for Navigation”. In: *Robotics: Science and Systems X*. Robotics: Science and Systems 2014. Robotics: Science and Systems Foundation, 12th July 2014. ISBN: 978-0-9923747-0-9. DOI: [10.15607/RSS.2014.X.047](https://doi.org/10.15607/RSS.2014.X.047).
- [274] N. J. Strausfeld. *Atlas of an Insect Brain*. Springer Berlin Heidelberg, 1976. 238 pp. ISBN: 978-3-540-07343-7. Google Books: [Vw9DAAAAYAAJ](https://books.google.com/books?id=Vw9DAAAAYAAJ).
- [275] Nicholas J. Strausfeld and Yongsheng Li. “Organization of Olfactory and Multimodal Afferent Neurons Supplying the Calyx and Pedunculus of the Cockroach Mushroom Bodies”. In: *Journal of Comparative Neurology* 409.4 (1999), pp. 603–625. ISSN: 1096-9861. DOI: [10.1002/\(SICI\)1096-9861\(19990712\)409:4<603::AID-CNE7>3.0.CO;2-P](https://doi.org/10.1002/(SICI)1096-9861(19990712)409:4<603::AID-CNE7>3.0.CO;2-P).
- [276] Nicholas J. Strausfeld et al. “Evolution, Discovery, and Interpretations of Arthropod Mushroom Bodies”. In: *Learning & Memory* 5.1 (May 1998), pp. 11–37. ISSN: 1072-0502. URL: <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC311242/> (visited on 07/06/2021).
- [277] Nicholas J. Strausfeld et al. “Ground Plan of the Insect Mushroom Body: Functional and Evolutionary Implications”. In: *Journal of Comparative Neurology* 513.3 (2009), pp. 265–291. ISSN: 1096-9861. DOI: [10.1002/cne.21948](https://doi.org/10.1002/cne.21948).
- [278] R. Strauss and M. Heisenberg. “A Higher Control Center of Locomotor Behavior in the Drosophila Brain”. In: *Journal of Neuroscience* 13.5 (1st May 1993), pp. 1852–1861. ISSN: 0270-6474, 1529-2401. DOI: [10.1523/JNEUROSCI.13-05-01852.1993](https://doi.org/10.1523/JNEUROSCI.13-05-01852.1993).

- [279] Wolfgang Stürzl and Jochen Zeil. “Depth, Contrast and View-Based Homing in Outdoor Scenes”. In: *Biological Cybernetics* 96.5 (25th Apr. 2007), pp. 519–531. ISSN: 0340-1200, 1432-0770. DOI: [10.1007/s00422-007-0147-3](https://doi.org/10.1007/s00422-007-0147-3).
- [280] Wolfgang Stürzl et al. “How Wasps Acquire and Use Views for Homing”. In: *Current Biology* 26.4 (Feb. 2016), pp. 470–482. DOI: [10.1016/j.cub.2015.12.052](https://doi.org/10.1016/j.cub.2015.12.052).
- [281] Wolfgang Stürzl et al. “Three-Dimensional Models of Natural Environments and the Mapping of Navigational Information”. In: *Journal of Comparative Physiology A* 201.6 (1st June 2015), pp. 563–584. ISSN: 1432-1351. DOI: [10.1007/s00359-015-1002-y](https://doi.org/10.1007/s00359-015-1002-y).
- [282] Xuelong Sun, Shigang Yue and Michael Mangan. “A Decentralised Neural Model Explaining Optimal Integration of Navigational Strategies in Insects”. In: *eLife* 9 (26th June 2020). Ed. by Mani Ramaswami, Michael B Eisen and Stanley Heinze, e54026. ISSN: 2050-084X. DOI: [10.7554/eLife.54026](https://doi.org/10.7554/eLife.54026).
- [283] Paul Szyszka, Alexander Galkin and Randolph Menzel. “Associative and Non-Associative Plasticity in Kenyon Cells of the Honeybee Mushroom Body”. In: *Frontiers in Systems Neuroscience* 2 (2008). ISSN: 1662-5137. DOI: [10.3389/neuro.06.003.2008](https://doi.org/10.3389/neuro.06.003.2008).
- [284] Alexandru Telea and Jarke J. van Wijk. “Visualization of Generalized Voronoi Diagrams”. In: *Data Visualization 2001*. Ed. by David S. Ebert, Jean M. Favre and Ronald Peikert. Eurographics. Vienna: Springer, 2001, pp. 165–174. ISBN: 978-3-7091-6215-6. DOI: [10.1007/978-3-7091-6215-6_18](https://doi.org/10.1007/978-3-7091-6215-6_18).
- [285] Hanne H. Thoen et al. “Insect-Like Organization of the Stomatopod Central Complex: Functional and Phylogenetic Implications”. In: *Frontiers in Behavioral Neuroscience* 11 (2017). ISSN: 1662-5153. DOI: [10.3389/fnbeh.2017.00012](https://doi.org/10.3389/fnbeh.2017.00012).
- [286] N. Tinbergen. *The Study of Instinct*. The Study of Instinct. New York, NY, US: Clarendon Press/Oxford University Press, 1951, pp. xii, 237. xii, 237.
- [287] Edward C. Tolman. “Cognitive Maps in Rats and Men”. In: *Psychological Review* 55.4 (1948), pp. 189–208. ISSN: 1939-1471(Electronic),0033-295X(Print). DOI: [10.1037/h0061626](https://doi.org/10.1037/h0061626).
- [288] Daniel Turner-Evans et al. “Angular Velocity Integration in a Fly Heading Circuit”. In: *eLife* 6 (22nd May 2017). Ed. by Alexander Borst, e23496. ISSN: 2050-084X. DOI: [10.7554/eLife.23496](https://doi.org/10.7554/eLife.23496).
- [289] Taro Ueno et al. “Identification of a Dopamine Pathway That Regulates Sleep and Arousal in *Drosophila*”. In: *Nature Neuroscience* 15.11 (11 Nov. 2012), pp. 1516–1523. ISSN: 1546-1726. DOI: [10.1038/nn.3238](https://doi.org/10.1038/nn.3238).
- [290] Andrew Vardy and Ralf Möller. “Biologically Plausible Visual Homing Methods Based on Optical Flow Techniques”. In: *Connection Science* 17.1-2 (Mar. 2005), pp. 47–89. ISSN: 0954-0091, 1360-0494. DOI: [10.1080/09540090500140958](https://doi.org/10.1080/09540090500140958).

- [291] Adrienn G. Varga and Roy E. Ritzmann. “Cellular Basis of Head Direction and Contextual Cues in the Insect Brain”. In: *Current Biology* 26.14 (25th July 2016), pp. 1816–1828. ISSN: 0960-9822. DOI: [10.1016/j.cub.2016.05.037](https://doi.org/10.1016/j.cub.2016.05.037).
- [292] Robert J. Vickerstaff and Allen Cheung. “Which Coordinate System for Modelling Path Integration?” In: *Journal of Theoretical Biology* 263.2 (21st Mar. 2010), pp. 242–261. ISSN: 0022-5193. DOI: [10.1016/j.jtbi.2009.11.021](https://doi.org/10.1016/j.jtbi.2009.11.021).
- [293] P. Viola and M. Jones. “Rapid Object Detection Using a Boosted Cascade of Simple Features”. In: *Proceedings of the 2001 IEEE Computer Society Conference on Computer Vision and Pattern Recognition. CVPR 2001*. 2001 IEEE Computer Society Conference on Computer Vision and Pattern Recognition. CVPR 2001. Vol. 1. Kauai, HI, USA: IEEE Comput. Soc, 2001, pp. I-511–I-518. ISBN: 978-0-7695-1272-3. DOI: [10.1109/CVPR.2001.990517](https://doi.org/10.1109/CVPR.2001.990517).
- [294] Pauli Virtanen et al. “SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python”. In: *Nature Methods* 17 (2020), pp. 261–272. DOI: [10.1038/s41592-019-0686-2](https://doi.org/10.1038/s41592-019-0686-2).
- [295] Karl von Frisch. “Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen”. In: *Experientia* 5.4 (1st Apr. 1949), pp. 142–148. ISSN: 1420-9071. DOI: [10.1007/BF02174424](https://doi.org/10.1007/BF02174424).
- [296] Karl von Frisch. *The Dance Language and Orientation of Bees*. The Dance Language and Orientation of Bees. Cambridge, MA, US: Harvard University Press, 1967.
- [297] J. von Uexküll. *Umwelt und Innenwelt der Tiere*. Berlin, Heidelberg: Springer Berlin Heidelberg, 1921. ISBN: 978-3-662-22877-7 978-3-662-24819-5. DOI: [10.1007/978-3-662-24819-5](https://doi.org/10.1007/978-3-662-24819-5).
- [298] E. J. Warrant and P. D. McIntyre. “Arthropod Eye Design and the Physical Limits to Spatial Resolving Power”. In: *Progress in Neurobiology* 40.4 (Apr. 1993), pp. 413–461. ISSN: 0301-0082.
- [299] Barbara Webb. “The Internal Maps of Insects”. In: *The Journal of Experimental Biology* 222 (Pt Suppl 1 2nd June 2019). ISSN: 1477-9145. DOI: [10.1242/jeb.188094](https://doi.org/10.1242/jeb.188094).
- [300] Barbara Webb and Antoine Wystrach. “Neural Mechanisms of Insect Navigation”. In: *Current Opinion in Insect Science*. Pests and Resistance * Behavioural Ecology 15 (1st June 2016), pp. 27–39. ISSN: 2214-5745. DOI: [10.1016/j.cois.2016.02.011](https://doi.org/10.1016/j.cois.2016.02.011).
- [301] Franz Weber, Christian K. Machens and Alexander Borst. “Spatiotemporal Response Properties of Optic-Flow Processing Neurons”. In: *Neuron* 67.4 (26th Aug. 2010), pp. 629–642. ISSN: 0896-6273. DOI: [10.1016/j.neuron.2010.07.017](https://doi.org/10.1016/j.neuron.2010.07.017).

-
- [302] Rainer Wegerhoff and Olaf Breidbach. “Structure and Development of the Larval Central Complex in a Holometabolous Insect, the Beetle *Tenebrio Molitor*”. In: *Cell and Tissue Research* 268.2 (1st May 1992), pp. 341–358. ISSN: 1432-0878. DOI: [10.1007/BF00318803](https://doi.org/10.1007/BF00318803).
- [303] R. Wehner. “The Ant’s Celestial Compass System: Spectral and Polarization Channels”. In: *Orientation and Communication in Arthropods*. Ed. by Miriam Lehrer. EXS. Basel: Birkhäuser, 1997, pp. 145–185. ISBN: 978-3-0348-8878-3. DOI: [10.1007/978-3-0348-8878-3_6](https://doi.org/10.1007/978-3-0348-8878-3_6).
- [304] R. Wehner and P. Duelli. “The Spatial Orientation of Desert Ants, *Cataglyphis Bicolor*, before Sunrise and after Sunset”. In: *Experientia* 27.11 (1971), pp. 1364–1366. ISSN: 00144754. DOI: [10.1007/BF02136743](https://doi.org/10.1007/BF02136743).
- [305] R. Wehner, A. C. Marsh and S. Wehner. “Desert Ants on a Thermal Tigh trope”. In: *Nature* 357.6379 (6379 June 1992), pp. 586–587. ISSN: 1476-4687. DOI: [10.1038/357586a0](https://doi.org/10.1038/357586a0).
- [306] R. Wehner, B. Michel and P. Antonsen. “Visual Navigation in Insects: Coupling of Egocentric and Geocentric Information”. In: *Journal of Experimental Biology* 199.1 (1st Jan. 1996), pp. 129–140. ISSN: 0022-0949, 1477-9145. URL: <https://jeb.biologists.org/content/199/1/129> (visited on 05/11/2019).
- [307] R. Wehner and F. Räber. “Visual Spatial Memory in Desert Ants, *Cataglyphis Bicoior* (Hymenoptera: Formicidae)”. In: *Experientia* 35.12 (Dec. 1979), pp. 1569–1571. ISSN: 0014-4754, 1420-9071. DOI: [10.1007/BF01953197](https://doi.org/10.1007/BF01953197).
- [308] Rüdiger Wehner. “‘Matched Filters’: Neural Models of the External World”. In: *Journal of Comparative Physiology A* 161.4 (1987), pp. 511–531. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/BF00603659](https://doi.org/10.1007/BF00603659).
- [309] Rüdiger Wehner. *Desert Navigator: The Journey of an Ant*. Harvard University Press, 7th Dec. 2019. 401 pp. ISBN: 978-0-674-04588-0. Google Books: [Z3jDDwAAQBAJ](https://books.google.com/books?id=Z3jDDwAAQBAJ).
- [310] Rüdiger Wehner. “Spatial Organization of Foraging Behavior in Individually Searching Desert Ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namib Desert)”. In: *From Individual to Collective Behavior in Social Insects*. EXS 54. Basel: Birkhäuser, 1987, pp. 15–42.
- [311] Rüdiger Wehner. “Taxonomie, Funktionsmorphologie Und Zoogeographie Der Saharischen Wüstennameise *Cataglyphis Fortis* (Forel 1902) Stat. Nov”. In: *Senckenbergiana biol* 64 (1983), pp. 89–132.
- [312] Rüdiger Wehner. “The Architecture of the Desert Ant’s Navigational Toolkit (Hymenoptera: Formicidae)”. In: (2009), p. 12.

- [313] Rüdiger Wehner, Christoph Meier and Christoph Zollikofer. “The Ontogeny of Foraging Behaviour in Desert Ants, *Cataglyphis Bicolor*”. In: *Ecological Entomology* 29.2 (Apr. 2004), pp. 240–250. ISSN: 0307-6946, 1365-2311. DOI: [10.1111/j.0307-6946.2004.00591.x](https://doi.org/10.1111/j.0307-6946.2004.00591.x).
- [314] Rüdiger Wehner and Wolfgang Rössler. “Chapter 39 - Bounded Plasticity in the Desert Ant’s Navigational Tool Kit”. In: *Handbook of Behavioral Neuroscience*. Ed. by Randolph Menzel and Paul R. Benjamin. Vol. 22. Invertebrate Learning and Memory. Elsevier, 1st Jan. 2013, pp. 514–529. DOI: [10.1016/B978-0-12-415823-8.00039-3](https://doi.org/10.1016/B978-0-12-415823-8.00039-3).
- [315] Rüdiger Wehner and Mandyam V Srinivasan. “Searching Behaviour of Desert Ants, Genus *Cataglyphis* (Formicidae, Hymenoptera)”. In: *Journal of comparative physiology* 142.3 (1981), pp. 315–338. DOI: [10.1007/BF00605445](https://doi.org/10.1007/BF00605445).
- [316] Rüdiger Wehner and Mandyam V. Srinivasan. “Path Integration in Insects”. In: *The Neurobiology of Spatial Behaviour*. Ed. by K.J. Jeffery. Oxford University Press, 6th Nov. 2003, pp. 9–30. ISBN: 978-0-19-851524-1. DOI: [10.1093/acprof:oso/9780198515241.003.0001](https://doi.org/10.1093/acprof:oso/9780198515241.003.0001).
- [317] Rüdiger Wehner and Sibylle Wehner. “Parallel Evolution of Thermophilia: Daily and Seasonal Foraging Patterns of Heat-Adapted Desert Ants: *Cataglyphis* and *Ocymyrmex* Species*”. In: *Physiological Entomology* 36.3 (2011), pp. 271–281. ISSN: 1365-3032. DOI: [10.1111/j.1365-3032.2011.00795.x](https://doi.org/10.1111/j.1365-3032.2011.00795.x).
- [318] Rüdiger Wehner et al. “Calibration Processes in Desert Ant Navigation: Vector Courses and Systematic Search”. In: *Journal of Comparative Physiology A* 188.9 (2002), pp. 683–693. DOI: [10.1007/s00359-002-0340-8](https://doi.org/10.1007/s00359-002-0340-8).
- [319] Peter T. Weir and Michael H. Dickinson. “Functional Divisions for Visual Processing in the Central Brain of Flying *Drosophila*”. In: *Proceedings of the National Academy of Sciences* 112.40 (6th Oct. 2015), E5523–E5532. ISSN: 0027-8424, 1091-6490. DOI: [10.1073/pnas.1514415112](https://doi.org/10.1073/pnas.1514415112).
- [320] Gerald Westheimer. “Center-Surround Antagonism in Spatial Vision: Retinal or Cortical Locus?” In: *Vision Research* 44.21 (1st Sept. 2004), pp. 2457–2465. ISSN: 0042-6989. DOI: [10.1016/j.visres.2004.05.014](https://doi.org/10.1016/j.visres.2004.05.014).
- [321] J. L. D. Williams. “Anatomical Studies of the Insect Central Nervous System: A Ground-Plan of the Midbrain and an Introduction to the Central Complex in the Locust, *Schistocerca Gregaria* (Orthoptera)”. In: *Journal of Zoology* 176.1 (1975), pp. 67–86. ISSN: 1469-7998. DOI: [10.1111/j.1469-7998.1975.tb03188.x](https://doi.org/10.1111/j.1469-7998.1975.tb03188.x).
- [322] Edward O. Wilson. *The Diversity of Life*. Questions of Science. Cambridge, Mass: Belknap Press of Harvard University Press, 1992. 424 pp. ISBN: 978-0-674-21298-5.

-
- [323] Edward O. Wilson. “The Little Things That Run the World (The Importance and Conservation of Invertebrates)”. In: *Conservation Biology* 1 (4, 1987), pp. 344–346. DOI: [10.1111/j.1523-1739.1987.tb00055.x](https://doi.org/10.1111/j.1523-1739.1987.tb00055.x). JSTOR: 2386020.
- [324] Matthias Wittlinger, Rüdiger Wehner and Harald Wolf. “The Ant Odometer: Stepping on Stilts and Stumps”. In: *Science* 312.5782 (30th June 2006), pp. 1965–1967. ISSN: 0036-8075, 1095-9203. DOI: [10.1126/science.1126912](https://doi.org/10.1126/science.1126912).
- [325] Harald Wolf and Rüdiger Wehner. “Pinpointing Food Sources: Olfactory and Anemotactic Orientation in Desert Ants, *Cataglyphis Fortis*”. In: *Journal of Experimental Biology* 203.5 (2000), pp. 857–868. ISSN: 00220949. DOI: [10.5167/uzh-636](https://doi.org/10.5167/uzh-636).
- [326] Harald Wolf, Matthias Wittlinger and Siegfried Bolek. “Re-Visiting of Plentiful Food Sources and Food Search Strategies in Desert Ants”. In: *Frontiers in neuroscience* 6 (2012), p. 102. DOI: [10.3389/fnins.2012.00102](https://doi.org/10.3389/fnins.2012.00102).
- [327] Tanya Wolff and Gerald M Rubin. “Neuroarchitecture of the *Drosophila* Central Complex: A Catalog of Nodulus and Asymmetrical Body Neurons and a Revision of the Protocerebral Bridge Catalog”. In: *Journal of Comparative Neurology* (2018). DOI: [10.1002/cne.24512](https://doi.org/10.1002/cne.24512).
- [328] A. Wystrach, G. Beugnon and K. Cheng. “Landmarks or Panoramas: What Do Navigating Ants Attend to for Guidance?” In: *Frontiers in Zoology* 8.1 (2011), p. 21. ISSN: 1742-9994. DOI: [10.1186/1742-9994-8-21](https://doi.org/10.1186/1742-9994-8-21).
- [329] A. Wystrach and S. Schwarz. “Ants Use a Predictive Mechanism to Compensate for Passive Displacements by Wind”. In: *Current Biology* 23.24 (16th Dec. 2013), R1083–R1085. ISSN: 0960-9822. DOI: [10.1016/j.cub.2013.10.072](https://doi.org/10.1016/j.cub.2013.10.072).
- [330] A. Wystrach et al. “Views, Landmarks, and Routes: How Do Desert Ants Negotiate an Obstacle Course?” In: *Journal of Comparative Physiology A* 197.2 (Feb. 2011), pp. 167–179. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/s00359-010-0597-2](https://doi.org/10.1007/s00359-010-0597-2).
- [331] Antoine Wystrach, Guy Beugnon and Ken Cheng. “Ants Might Use Different View-Matching Strategies on and off the Route”. In: *The Journal of Experimental Biology* 215 (Pt 1 1st Jan. 2012), pp. 44–55. ISSN: 1477-9145. DOI: [10.1242/jeb.059584](https://doi.org/10.1242/jeb.059584).
- [332] Antoine Wystrach and Paul Graham. “What Can We Learn from Studies of Insect Navigation?” In: *Animal Behaviour* 84.1 (1st July 2012), pp. 13–20. ISSN: 0003-3472. DOI: [10.1016/j.anbehav.2012.04.017](https://doi.org/10.1016/j.anbehav.2012.04.017).
- [333] Antoine Wystrach, Michael Mangan and Barbara Webb. “Optimal Cue Integration in Ants”. In: *Proceedings of the Royal Society B: Biological Sciences* 282.1816 (7th Oct. 2015), p. 20151484. DOI: [10.1098/rspb.2015.1484](https://doi.org/10.1098/rspb.2015.1484).

- [334] Antoine Wystrach et al. “How Do Field of View and Resolution Affect the Information Content of Panoramic Scenes for Visual Navigation? A Computational Investigation”. In: *Journal of Comparative Physiology A* 202.2 (Feb. 2016), pp. 87–95. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/S00359-015-1052-1](https://doi.org/10.1007/S00359-015-1052-1).
- [335] Antoine Wystrach et al. “Multiple Sources of Celestial Compass Information in the Central Australian Desert Ant *Melophorus Bagoti*”. In: *Journal of Comparative Physiology A* 200.6 (1st June 2014), pp. 591–601. ISSN: 1432-1351. DOI: [10.1007/s00359-014-0899-x](https://doi.org/10.1007/s00359-014-0899-x).
- [336] Antoine Wystrach et al. “Rapid Aversive and Memory Trace Learning during Route Navigation in Desert Ants”. In: *Current Biology* (Apr. 2020), S096098222030289X. ISSN: 09609822. DOI: [10.1016/j.cub.2020.02.082](https://doi.org/10.1016/j.cub.2020.02.082).
- [337] Antoine Wystrach et al. “Running Paths to Nowhere: Repetition of Routes Shows How Navigating Ants Modulate Online the Weights Accorded to Cues”. In: *Animal Cognition* 22.2 (1st Mar. 2019), pp. 213–222. ISSN: 1435-9456. DOI: [10.1007/s10071-019-01236-7](https://doi.org/10.1007/s10071-019-01236-7).
- [338] Antoine Wystrach et al. “Snapshots in Ants? New Interpretations of Paradigmatic Experiments”. In: *Journal of Experimental Biology* 216.10 (15th May 2013), pp. 1766–1770. ISSN: 0022-0949. DOI: [10.1242/jeb.082941](https://doi.org/10.1242/jeb.082941).
- [339] Antoine Wystrach et al. “Visual Scanning Behaviours and Their Role in the Navigation of the Australian Desert Ant *Melophorus Bagoti*”. In: *Journal of Comparative Physiology A* 200.7 (July 2014), pp. 615–626. ISSN: 0340-7594, 1432-1351. DOI: [10.1007/s00359-014-0900-8](https://doi.org/10.1007/s00359-014-0900-8).
- [340] T. Zars. “Behavioral Functions of the Insect Mushroom Bodies”. In: *Current Opinion in Neurobiology* 10.6 (Dec. 2000), pp. 790–795. ISSN: 0959-4388. DOI: [10.1016/S0959-4388\(00\)00147-1](https://doi.org/10.1016/S0959-4388(00)00147-1).
- [341] J. Zeil, A. Narendra and W. Sturzl. “Looking and Homing: How Displaced Ants Decide Where to Go”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 369.1636 (6th Jan. 2014), pp. 20130034–20130034. ISSN: 0962-8436, 1471-2970. DOI: [10.1098/rstb.2013.0034](https://doi.org/10.1098/rstb.2013.0034).
- [342] Jochen Zeil. “Visual Homing: An Insect Perspective”. In: *Current Opinion in Neurobiology. Neuroethology* 22.2 (1st Apr. 2012), pp. 285–293. ISSN: 0959-4388. DOI: [10.1016/j.conb.2011.12.008](https://doi.org/10.1016/j.conb.2011.12.008).
- [343] Jochen Zeil and Pauline N Fleischmann. “The Learning Walks of Ants (Hymenoptera: Formicidae)”. In: *Myrmecological News* 29 (24th July 2019), pp. 93–110. ISSN: 1997-3500. DOI: [10.25849/myrmecol.news_029:093](https://doi.org/10.25849/myrmecol.news_029:093).
- [344] Jochen Zeil, Martin I. Hofmann and Javaan S. Chahl. “Catchment Areas of Panoramic Snapshots in Outdoor Scenes”. In: *JOSA A* 20.3 (1st Mar. 2003), pp. 450–469. ISSN: 1520-8532. DOI: [10.1364/JOSAA.20.000450](https://doi.org/10.1364/JOSAA.20.000450).

Appendix A

The role of attractive and repellent scene memories in ant homing (*Myrmecia croslandi*)

Trevor Murray, Zoltán Kócsi, Hansjürgen Dahmen, Ajay Narendra, Florent Le Moël, Antoine Wystrach and Jochen Zeil



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RESEARCH ARTICLE

The role of attractive and repellent scene memories in ant homing (*Myrmecia croslandi*)

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ABSTRACT

Solitary foraging ants rely on vision when travelling along routes and when pinpointing their nest. We tethered foragers of *Myrmecia croslandi* on a trackball and recorded their intended movements when the trackball was located on their normal foraging corridor (on-route), above their nest and at a location several metres away where they have never been before (off-route). We found that at on- and off-route locations, most ants walk in the nest or foraging direction and continue to do so for tens of metres in a straight line. In contrast, above the nest, ants walk in random directions and change walking direction frequently. In addition, the walking direction of ants above the nest oscillates on a fine scale, reflecting search movements that are absent from the paths of ants at the other locations. An agent-based simulation shows that the behaviour of ants at all three locations can be explained by the integration of attractive and repellent views directed towards or away from the nest, respectively. Ants are likely to acquire such views via systematic scanning movements during their learning walks. The model predicts that ants placed in a completely unfamiliar environment should behave as if at the nest, which our subsequent experiments confirmed. We conclude first, that the ants' behaviour at release sites is exclusively driven by what they currently see and not by information on expected outcomes of their behaviour; and second, that navigating ants might continuously integrate attractive and repellent visual memories. We discuss the benefits of such a procedure.

KEY WORDS: Visual navigation, Ants, Attractive and repellent memories, Homing, Route following, *Myrmecia croslandi*

INTRODUCTION

Navigation on a local scale, in contrast to that on a global scale, involves travelling along memorized routes and pinpointing places (e.g. Zeil, 2012). Much evidence has accumulated to show that ants form visual memories of how the scene looks along routes (e.g. Wehner et al., 1996; Wystrach et al., 2011a,b; Mangan and Webb, 2012) and that alignment matching (Zeil et al., 2003; Collett et al., 2013) between memorized and currently experienced views

provides robust information on heading direction (Graham and Cheng, 2009; Baddeley et al., 2011, 2012; Narendra et al., 2013; Zeil et al., 2014). Heading direction can be recovered, even from locations at some distance from familiar locations, by detecting the minimum of the rotational image difference function (rotIDF) resulting from a comparison between current and memorized views (Zeil et al., 2003; Stürzl and Zeil, 2007; Philippides et al., 2011; Narendra et al., 2013; Stürzl et al., 2015). This minimum provides a measure of familiarity in addition to a heading direction (Baddeley et al., 2011, 2012; Graham et al., 2010).

Before becoming foragers, ants perform a series of learning walks around the nest during which they alternate between turning to look in the nest direction (Müller and Wehner, 2010; Fleischmann et al., 2016, 2017, 2018a,b) and in directions away from the nest from different compass directions (Jayatilaka et al., 2018; reviewed in Zeil and Fleischmann, 2019). It is attractive to assume that the ants store snapshots during these turns whenever they are aligned parallel to the home vector – that is, when they are facing toward or away from the nest (Müller and Wehner, 2010; Graham et al., 2010; Jayatilaka et al., 2018) – as this is theoretically sufficient for returning ants to align with and walk in the direction of the most familiar of nest-directed snapshots in order to pinpoint the nest (Graham et al., 2010; Baddeley et al., 2012; Wystrach et al., 2013a).

Such visual alignment matching (Collett et al., 2013) explains well how ants recover the correct direction when on their familiar route (Wystrach et al., 2011a,b, 2012; Baddeley et al., 2012; Kodzhabashev and Mangan, 2015). Moreover, nest-directed views acquired during learning walks (reviewed in Collett and Zeil, 2018; Zeil and Fleischmann, 2019) can also provide guidance from locations that are unfamiliar to ants and that can be 10–15 m away from the nest in open forest habitats (Narendra et al., 2013; Stürzl et al., 2015), although the initial movements of released ants may not be directed toward the nest (Zeil et al., 2014), but toward a familiar route (Collett et al., 2007; Wystrach et al., 2012).

Overall, this line of work has led to the suggestion that visually navigating insects would only need 'procedural knowledge' about where to go rather than a more sophisticated representation of their spatial environment that would allow them 'to know where they are' (Collett et al., 2002; Wehner et al., 2006; Cheung et al., 2014; Graham and Philippides, 2017).

To test this directly, we positioned ants that we had tethered over a trackball at different locations in their natural foraging environment, including above their nest, and recorded their intended direction and distance of movement. Ants mounted on the ball were well oriented towards the nest at both on- and off-route locations, but displayed a search pattern when above the nest, as if they knew they were at the nest, implying a sort of positional rather than just procedural knowledge. Using a simple agent-based simulation we show, however, that these results can be more parsimoniously explained by alignment matching involving continuous integration of

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attractive and repellent visual memories, acquired when facing, respectively, towards and away from the nest during learning walks.

MATERIALS AND METHODS

Ants and experimental site

We worked with foragers of the Australian jack jumper ant *Myrmecia croslandi* Taylor 1991 from a nest in the Australian National University's campus field station ($-35^{\circ}16'49.87''\text{S}$ and $149^{\circ}06'43.74''\text{E}$). The ants are day-active, visually navigating solitary foragers that hunt for insects on the ground at up to 4 m distance from the nest and on trees about 12 m away from the nest where they also feed on sugar secretions of plant-sucking insects (see Fig. 2A, centre). For details of the foraging ecology and the navigational abilities of these ants, see Jayatilaka et al. (2011, 2014), Narendra et al. (2013) and Zeil et al. (2014). During February to March 2017 and December 2017 to March 2018, between 09:00 h and 15:00 h, we caught foraging ants either at their foraging trees about 12 m from the nest in a 'full-vector' state (FV, $n=10$) or at the nest in a 'zero-vector' state (ZV, $n=18$), offered them sugar water solution to feed on, before immobilizing them on ice for up to 15 min and tethering them to a metal pin by their mesonotum (thorax) using Bondic liquid plastic welder (Biochem Solutions, Ellerslie, New Zealand). The ants were placed on an air-cushioned light-weight, 5 cm diameter track ball (Fig. 1A) on which they were free to rotate around the yaw axis but that allowed us to record their intended translational movements as described in detail by Dahmen et al. (2017). We placed the trackball contraption with a tethered ant at each of three locations in a random order (Fig. 2 A, centre): 6.5 m west of the nest where none of the ants were likely to have been before (off-route); 6.5 m south of the nest, half-way along their normal foraging route towards trees (on-route); and directly above the nest (nest).

We recorded the intended movement directions and distances on the trackball at each displacement for up to 10 min, before shifting the track ball contraption together with the tethered ant to the next location. Ants were carefully un-tethered and released close to the nest following the three displacements.

To demonstrate the foraging patterns of ants at this nest and the full range of learning walks, we show the paths of foraging ants, ants that performed learning walks and ants that were released after contributing to unrelated experiments that were recorded with differential GPS (DGPS) over 2 years (Fig. 2A, centre; Fig. S1; for details, see Narendra et al., 2013). In brief, coloured flag pins were placed on the ground approximately 20 cm behind a walking ant at fairly regular intervals, carefully avoiding disturbing her progress. The resulting pin trail was subsequently followed with the rover antenna of a DGPS system, recording the position with an accuracy of better than 10 cm.

Requests for further information and for original data should be directed to the corresponding author (T.M.).

Data analysis

We recorded trackball rotations due to the intended translation of the ants at $275 \text{ frames s}^{-1}$, which reflect the direction and speed of the ants' intended movements. We present the reconstructed paths, final bearings, changes in walking direction and path lengths for the first 5 min of recordings at the three displacement locations. With the exception of one ant at the off-route location, all ants reached this criterion. We used the Matlab (MathWorks, Natick, MA, USA) circular statistics toolbox (by Philipp Berens) to perform Rayleigh's test for non-uniformity on directional data and Wilcoxon rank sum tests on differences between displacement locations using the

ranksum function in Matlab. For comparisons between all three locations, we applied a Bonferroni correction with a resulting critical value for individual tests of $P=0.0167$.

Agent-based modelling

Reconstructed world and ant views

We rendered panoramic views within a 3D model of the ants' natural environment that was previously reconstructed at the ANU Campus Field Station using a laser scanner and camera-based methods (Stürzl et al., 2015). We down-sampled the rendered views to 360×180 pixels; that is, 1 deg per pixel resolution to roughly match the resolution of the ants' compound eyes. Note that the 3D model was obtained 3 years before the treadmill experiments were conducted, so there will be some changes to the landmark panorama, in particular involving the canopy, while all the major geometric relationships of dominant visual features such as trees will have remained the same.

Memorized views and current familiarity

The simulated ant (agent) is assumed to have stored a collection of memorized views around the nest during learning walks and along its normal foraging route (Fig. 1B). During tests, the agent computes a value of visual familiarity at each time step by comparing the current view with its memory bank. This is achieved by calculating the global root mean squared pixel difference (Zeil et al., 2003) between the current view and each of the views in the memory bank, and keeping the value of the lowest mismatch, as is typically done in models and studies of ant navigation (Wystrach et al., 2011a,b, 2012; Baddeley et al., 2011, 2012; Philippides et al., 2011; Narendra et al., 2013; Zeil et al., 2014; Stürzl et al., 2015). Because high mismatch values indicate a large discrepancy between the current and a memorized view, the value indicates the current unfamiliarity score rather than a familiarity score. Note that in the insect brain, the activity of the mushroom body output neurons (MBON) also correlate with unfamiliarity rather than familiarity (Owald et al., 2015; Felsenberg et al., 2018). Importantly, views in this model are not rotated, but compared only at the facing direction of the current and memorized views. That is, the agent does not need to stop and scan because only one view is compared for each step.

Combining attractive and repellent visual memories

The novel aspect of the current model is that the agent is assumed to have two independent memory banks (Fig. 1B–D): one containing attractive views and one containing repellent views. Both memory banks contain views experienced during learning and foraging walks; the attractive memory bank contains views that are assumed to have been memorized when the ants were oriented toward the nest and the repellent memory bank contains those that have been memorized while looking away from the nest. This is motivated by the very regular scanning movements of ants during their learning walks where they alternate looking towards the nest and away from the nest direction (Jayatilaka et al., 2018; Zeil and Fleischmann, 2019). For simplicity, learning walk views were assumed to have been acquired within a 1 m radius around the nest and we chose a 10 m long route, corresponding roughly with the foraging corridor of this particular nest (see Fig. 2A, centre). Both nest-directed (attractive) learning walk views and views away from the nest (repellent) were taken from positions along a spiral rather than a circle around the nest (Fig. 1B), to mimic the fact that successive learning walk loops reach increasing distances from the nest (e.g. Fleischmann et al., 2016; Jayatilaka et al., 2018) and to ensure that results at the nest were not dependent on having views memorized at

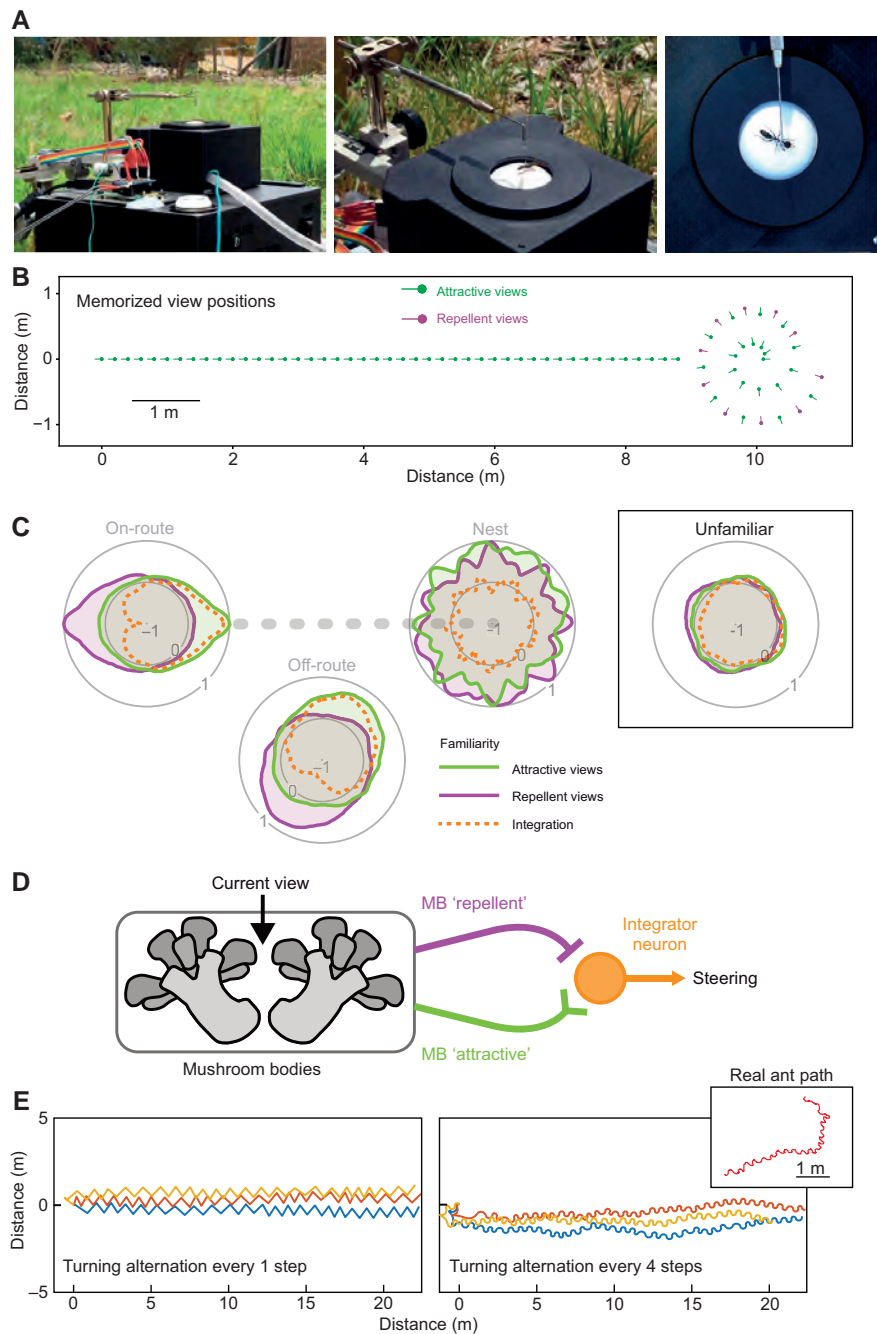


Fig. 1. Experimental set-up and agent-based modelling. (A) Three views of the air-cushioned trackball contraption and the tethered ant. (B) Schematic map of the attractive and repellent memorized views along the foraging route and around the nest that constituted the attractive and repellent memory bank. (C) Schematic distribution of familiarity (0=unfamiliar; 1=familiar) for attractive and repellent views at the four release locations and the result of their integration (+1=attractive; 0=neutral; -1=repellent). Note that, after integration (orange dash-line), distributions at the nest and at the completely unfamiliar site are neutral for different reasons: views at the nest are familiar for both attractive and repellent pathways, which cancel each other; while views at the completely unfamiliar site are unfamiliar for both pathways. (D) A 'neuro-schematic' summary of the model comparing a current view with a repellent and an attractive view memory bank (MB), and the integration of the output providing a steering command. (E) The paths generated by the simulation reproduce the details of real ant paths better when the regular alternation of path direction is implemented every 4th step, rather than at each successive step (as was done in the present study); however, this has no impact on the model's overall trajectory.

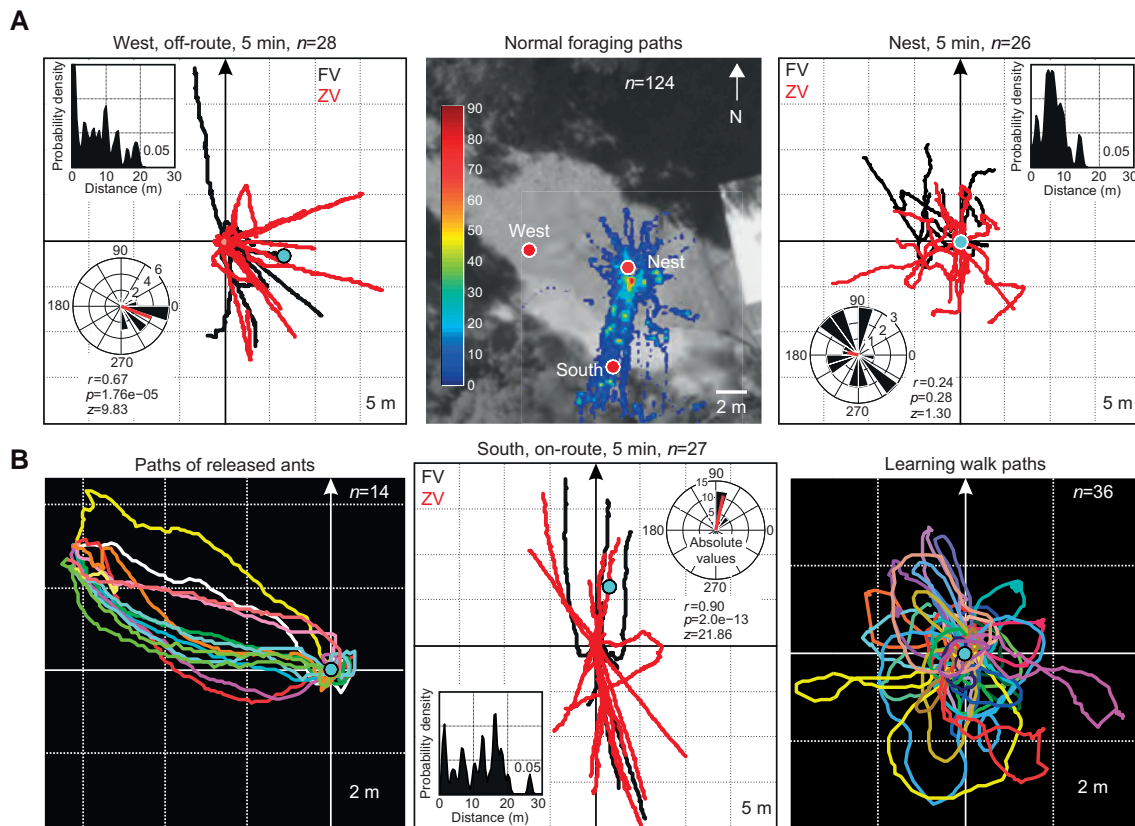


Fig. 2. The behaviour of tethered ants at three locations in their natural foraging environment. (A) Aerial photograph (centre) of the nest area with off-route, nest and on-route locations marked by red circles. False colour-coded area shows the 2D probability density of 124 outward going paths of foraging ants that operated from this nest and were tracked with differential GPS (DGPS) over a period of 2 years. See colour bar for scale and Fig. S1 for individual paths. Intended paths of tethered ants are shown for the off-route location (A, left), the nest location (A, right) and the on-route location (B, centre), with the paths of zero-vector (ZV) ants shown in red and those of full-vector (FV) ants in black. The nest location is indicated by a blue circle. Insets show for both FV and ZV ants the probability density of virtual distances from the starting point reached after 5 min and circular histograms of final bearings with the red line indicating the length and direction of the mean vector; r , resulting vector length; p , probability of rejecting hypothesis of uniform distribution; z : z-statistic of Rayleigh test of uniformity. (B) Left: paths of 14 ants released just north of the off-route location and tracked with DGPS. Right: learning walk paths of ants around the nest, recorded with DGPS.

the exact same distance from the nest. We also included in the attractive memory bank views that foragers experience when travelling back to the nest along their normal foraging corridor (Fig. 1B).

Modelling procedure

At each time step, the agent computes two values of unfamiliarity: one by comparing the current view with the attractive memory bank and one by comparing the same current view with the repellent memory bank (Fig. 1C,D). These two unfamiliarity values are assumed to have an antagonistic effect on the agent's behaviour by turning it towards attractive and away from repellent stimuli, with the balance between the two drives determining the agent's turning amplitude. We modelled this by a simple subtraction resulting in a raw overall drive:

$$\text{Raw overall drive} = (\text{attractive unfamiliarity value} - \text{repellent unfamiliarity value})/0.2. \quad (1)$$

We normalized the value of this drive by always using the same value (0.2 in our world), corresponding roughly to the unfamiliarity score obtained between views from locations in the virtual world that are far apart, so that raw overall drive will be contained between -0.5 and 0.5 . A negative value thus indicates that 'attractive unfamiliarity' < 'repellent unfamiliarity'. A positive value indicates that 'attractive unfamiliarity' > 'repellent unfamiliarity'. We then transformed raw overall drive into overall drive with values ranging from 0 to 1 using a simple sigmoid function:

$$\text{Overall drive} = \text{sigmoid}(\text{raw overall drive}). \quad (2)$$

As a result, the overall drive tends towards 0 if 'attractive unfamiliarity' < 'repellent unfamiliarity', towards 1 if 'attractive unfamiliarity' > 'repellent unfamiliarity' and is 0.5 if 'attractive unfamiliarity' = 'repellent unfamiliarity'. In other words, a low score indicates that the current view matches a view in the attractive memory bank better than in the repellent memory bank and a high score indicates that the current view matches a view in the

repellent memory bank better than in the attractive memory bank (Fig. 1C).

To drive the agent, we used a similar approach to Kodzhabashev and Mangan (2015). The agent is a simple dot in space (x,y) with a current heading (θ). The agent has a continuously running oscillator alternating between left mode and right mode, which controls the current turning direction. For simplicity, we modelled this by alternating the turning direction at each time step (left–right–left–right) as in Kodzhabashev and Mangan (2015). The resulting paths typically show sharp zigzags; however, it is worth noting that alternating turning direction every 4th step produces smoother oscillations that better resemble real ant paths (Fig. 1E).

Turn direction is thus purely controlled by the oscillator; however, the turn amplitude (deg) is directly dependent on the current overall drive (see above): that is, on the current view familiarities:

$$\text{Turn amplitude} = \text{gain} \times \text{overall drive}. \quad (3)$$

We used a single parameter (gain) to convert the overall drive (between 0 and 1) into the angular value for the turn amplitude. We used gain=180, so that the turning amplitude would vary between 0 deg (if overall drive=0) and 180 deg (if overall drive=1), with 90 deg if overall drive=0.5, i.e. if attractive and repellent unfamiliarity values are equal.

Across time steps (n), the agent orientation (θ) will thus alternate between left and right turns $[(-1)^n]$, with each turn varying between 0 and 180 deg:

$$\theta(n+1) = \theta(n) + [\text{turn amplitude} \times (-1)^n] + \text{noise}. \quad (4)$$

To ensure that the agent is robust against the intrinsic noise of the real world, we added noise at each time step, as a random angular value drawn from a Gaussian distribution (mean=0; s.d.=10 deg).

Requests for the python code for the model should be directed to A.W.

Agent on a fictive treadmill

We simulated agent behaviour on a fictive treadmill by preventing forward motion. That is, at each time step we assumed that the agent (1) obtains the current view and computes its overall drive (Eqns 1 and 2); and (2) turns on the spot with turn direction determined by the state of the oscillator and turn amplitude (Eqns 3 and 4). As the location at which the agent is standing does not change, the view perceived at each time step only varies depending on the agent's current orientation. The agent on the treadmill was tested at different release locations and we recorded the resulting behaviour.

Using attractive visual memories only

We also tested the agent using the attractive memory bank only. In that case:

$$\text{Raw overall drive} = \text{attractive unfamiliarity}/0.2 - 0.5. \quad (5)$$

Given that attractive unfamiliarity is always positive, we removed 0.5 during normalization to centre the raw overall drive on 0, ranging roughly from -0.5 to 0.5 in the same way as when combining attractive and repellent memories. We then used the same sigmoid function to obtain an overall drive between 0 and 1 (Eqn 2).

RESULTS

Myrmecia croslandi ants released on the treadmill

Irrespective of whether they were caught in a ZV or FV state, tethered ants behaved differently when placed 6.5 m west of the nest (off-route; Fig. 2A, left), 6.5 m south of the nest (on-route; Fig. 2B, middle) or over the nest (nest; Fig. 2A, right).

In the off-route and on-route locations, most intended paths of both ZV and FV ants were goal directed either to the nest or to the individuals' specific foraging trees (see inset circular histograms in Fig. 2). This is to be expected for *M. croslandi* foragers, which ignore path integration information in the FV state as long as the landmark panorama provides navigational information (see Narendra et al., 2013; Zeil et al., 2014). The paths tended to be straight (see Fig. 3D). In contrast, over the nest, ZV ants moved in random directions, while FV ants tended to move roughly along the home vector direction to the north (at 90 deg; Fig. 2A, right, black tracks; see also Fig. 3B). Both ZV and FV ants at the nest changed their walking direction frequently. Inset histograms show that most tethered ants over the nest ended up after 5 min at final virtual distances less than 10 m from the nest (median 6.07 m), while at the on-route location, most ants reached much larger virtual distances (median 12.61 m) in the same amount of time (Wilcoxon rank sum test: nest versus on-route distances are different: $P=0.0045$, $z=2.8378$; see Fig. S2A). The median distances reached at the off-route location were not larger than the ones at the nest (median 6.2 m), owing to a conspicuous peak at small distances contributed by ants that were lost at this location.

The behaviour of ants at the off-route location is interesting primarily because most ants are home directed despite it being unlikely that they have ever been to this location before (see inset circular histogram, Fig. 2A, left). A heat map of the foraging movements of 124 ants from this nest that had been DGPS tracked on their outward foraging trips over 2 years shows that no ant had moved off-route of the nest for more than a few metres (Fig. 2A, middle). Some of the tethered ants appeared to have headed towards their foraging trees or the foraging corridor in a south-easterly direction; however, when we tracked ants that were released just north of the off-route location, many did initially walk for 2 m or so in a south-easterly direction before turning east toward the nest (Fig. 2B, left). Tethered ants at the off-route location must therefore get their bearing by comparing what they currently see with nest-directed views they are likely to have gathered during their learning walks, which can extend up to 4 m from the nest (Fig. 2B, right; see also Jayatilaka et al., 2018).

Both FV and ZV ants at the on-route location decided to move either back toward the nest or south toward their foraging trees (Fig. 2B, centre). Otherwise, they moved in a similar way to when at the off-route location. Most of them moved fast, straight and for distances far exceeding those needed to reach the nest or the trees.

The most conspicuous feature of paths at the nest location is the fact that the initial walking direction of ZV ants was random, while that of FV ants was in the general home vector direction (north) and that both ZV and FV ants changed walking direction frequently.

We quantified these differences between locations in three ways (see Fig. 3), considering final bearings, the relationship between path length and distance reached, and changes in walking direction. Fig. 3A shows the initial paths of ants at the three locations in more detail to emphasize the different behaviours and to highlight the additional fact that paths are fairly smooth at the off-route and on-route locations, but show a distinct sinusoidal oscillation at the nest location. With the exception of the bearings of ZV ants at the nest (Fig. 3C, right) and those of FV ants after 5 min at the off-route and

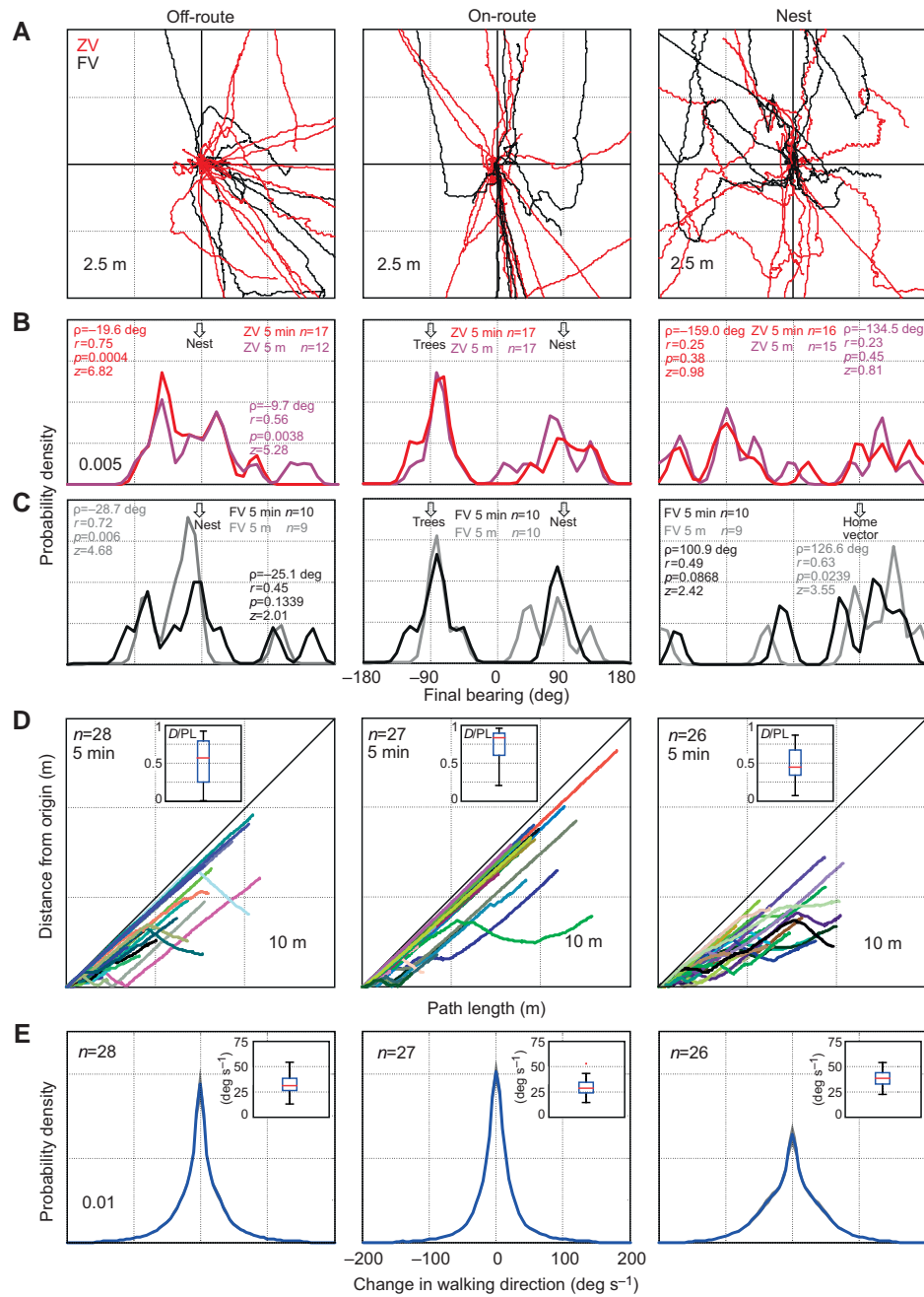


Fig. 3. Quantitative analysis of behavioural differences at the off-route, on-route and nest location. (A) Initial intended paths of tethered ants at a finer scale. The paths of ZV ants are shown in red and those of FV ants are in black. (B) Distribution of final bearings of ZV ants after 5 min (red) or having reached a virtual distance of 5 m from the start (purple) at the three locations. Probability densities were determined with 9 deg bandwidth of the kernel smoothing window; North is at +90 deg. Inset numbers show results of circular statistics (Rayleigh test of uniformity); ρ , mean vector direction; r , mean vector length; p , probability of uniformity; z , z-statistic. Arrows mark the direction of the nest and trees. (C) Distribution of final bearings for FV ants after 5 min (black) or having reached a virtual distance of 5 m from the start (grey). Arrows mark the direction of nest, trees and home vector. Other conventions as in B. (D) Distance from start over path length (PL) for the first 5 min of paths at the three locations. Paths are randomly coloured. Insets show boxplots with red median marked for the ratios of distance over path length at the end of 5 min. See Fig. S2B for statistics. (E) Distribution of changes in walking direction for all 5 min paths at the three locations. Shown are the means of individual distributions (blue) and standard errors (in grey – not visible). Insets show boxplots for the distributions of individual means. See Fig. S2C,D for statistics.

the nest location (Fig. 3C, left and right), the virtual bearings of ants after 5 min or at 5 m distance from the start were all significantly different from uniform distributions, both for ZV ants (Fig. 3B) and FV ants (Fig. 3C). While the distributions were unimodal for the off-route and nest location (see insets in Fig. 3B,C for circular statistics), they were clearly bimodal at the on-route location.

One measure of the straightness of paths is the way in which the straight-line distance from the start depends on path length (Fig. 3D), with straight paths without changes in direction lying close to the line of equality. After 5 min, the distribution of the ratios of final distance to final path length differed between the sites (see Fig. 3D inset; Fig. S2B inset) with the on-route paths being significantly straighter with a median ratio of distance over path length of 0.83, compared with 0.62 at the off-route location and of 0.45 at the nest location (Wilcoxon rank sum test at 5% significance level: on-route versus off-route: $P=0.0110$; on-route versus nest: $P=8.4992e^{-4}$; off-route versus nest: $P=0.6$; see Fig. S2B).

Finally, the behaviour of ants at the three sites also differed on a finer scale: the distribution of changes in path direction was much broader at the nest site, compared with the off-route and on-route location (Fig. 3E), reflecting the conspicuous oscillations of ant paths over the nest (see Fig. 3A, right). Note that these distributions had very long tails due to spikes of very high angular velocity which may be artefacts of trackball rotations when the ants were moving very slowly (see time series in Fig. 4). To test whether changes in path direction were indeed systematically larger at the nest location, we calculated the means of their absolute values at 11 frames s^{-1} over the first 5 min of walking for each ant and compared their distributions, both for angular velocities smaller than 200 deg s^{-1} (Fig. 3E inset; Fig. S2C inset) and for all angular velocities (Fig. S2D). Below 200 deg s^{-1} , nest paths were indeed wigglier compared with on-route paths (Fig. S2C; Wilcoxon rank sum test: nest versus on-route $P=2.56e^{-4}$, $z=-3.6563$), with the difference between nest and off-route location just failing to reach significance (nest versus off-route $P=0.019$, $z=-2.3458$). Considering the whole range of angular velocities (Fig. S2D), there was no difference between nest and the other locations, mainly because of the high angular velocities exhibited by ants at all sites.

We note that many ants at various times during the first 5 min on the trackball over the nest showed very regular path oscillations as documented in Fig. 3A and for three examples in Fig. 4 (red traces). The distribution and the time course of changes in path direction over the nest were different from those exhibited by the same ants at the on-route location (shown in blue in Fig. 4). Regular and sustained path oscillations led to periodicities in the auto-correlation function of changes in path direction and could be detected in 13 out of 25 cases of ants participating in all three locations (blue traces in Fig. S3), compared with 4/25 at the off-route location (red traces in Fig. S3) and 1/25 at the on-route location (green traces in Fig. S3). We add the caveat that the statistics of path properties are unlikely to be stationary during an experiment and that this particular aspect of ant behaviour will require future attention.

Agent-based modelling

To model the agent on a fictive treadmill, we prevented it from stepping forward, so that views were always perceived from the same spot, and were rotated according to the agent's current facing direction. We released the agent at four locations.

When tested close to the beginning of the homing route (on-route paths), the agent oriented mostly in the correct direction; that is, along the route towards the nest (blue paths in Fig. 5A). This is because the overall drive is close to 0 while facing in this direction

[the attractive unfamiliarity is very low and the repellent unfamiliarity is high (Fig. 1C) yielding very small turns (Fig. 5B,C)]. Note that if the agent happened to face in the opposite direction (as a result of noise), the overall drive would strongly increase and thus trigger a large turn.

When released away from the route (off-route paths), the agent also favoured one direction, indicating that this direction provided a smaller overall drive (yellow paths in Fig. 5A). This is an indication that the view at the off-route location and the nest-directed learning walk views were most familiar because their comparison produced a detectable minimum of the rotIDF and that the agent thus favoured a direction roughly pointing towards the nest.

When released on top of the nest (nest paths), the agent produced convoluted paths with no preferred direction (red paths in Fig. 5A). This is due to the rather uniform distribution of visual familiarities across directions (see Fig. 1C). At a more local scale, the paths showed much larger turn amplitudes than at the on-route or off-route paths (Fig. 5B,C). This is because, at the nest location, attractive and repellent memorized views provided a roughly equal match whatever the current facing direction, resulting in an overall drive around 0.5, thus yielding turns that were larger than when attractive and repellent memories matched best for different directions (see Fig. 1C).

When released at a distant unfamiliar location (distant path), the agent displayed equally large turn amplitudes to those at the nest (marked in black in Fig. 5A–C) because, as for the nest location, the attractive and the repellent memory bank provided roughly equal unfamiliarity values, thus resulting in an average overall drive around 0.5.

In contrast, when using the attractive memory bank only, turn amplitudes were large at the distant unfamiliar location (black) but comparatively low at the nest (red, Fig. 5, right). This is because the unfamiliarity value is high in the unfamiliar location (yielding a strong directional drive and thus large turns), and low at the nest because of the good match with learning walk views (yielding a low directional drive and thus small turns).

Testing model predictions with *M. croslandi*

Motivated by the different simulation results when using 'attractive only' and 'attractive/repellent' memory banks as well as by the rather counter-intuitive outcome that the use of attractive/repellent memories predicts a similar behaviour at the familiar nest location and at a completely unfamiliar location, we released *M. croslandi* ants mounted on the trackball both at the nest and at a distant location about 50 m south-west of the nest. The location was far beyond the ants' foraging trees and thus was likely to be completely unfamiliar to the ants. Strikingly, ants at this distant release location behaved in a similar way to that at the nest, both in terms of the ratio between the distance reached after 5 min and the path length (see box plot insets in Fig. 6A, centre; Wilcoxon rank sum test unfamiliar versus nest location: $P=0.7984$, ranksum=71) and in terms of the mean absolute change in walking direction (see box plot insets in Fig. 6A, right; Wilcoxon rank sum test unfamiliar versus nest location: $P=0.9591$, ranksum=67). The ants at both the unfamiliar and the nest site also displayed the characteristic path oscillations we observed at the nest in our previous experiments (compare Fig. 6A, B with Fig. 4), as predicted by the attractive/repellent model.

DISCUSSION

Our behavioural experiments revealed three fundamental properties of visual navigation in ants that could only be uncovered using the trackball method. First, we determined that whether on-route or off-

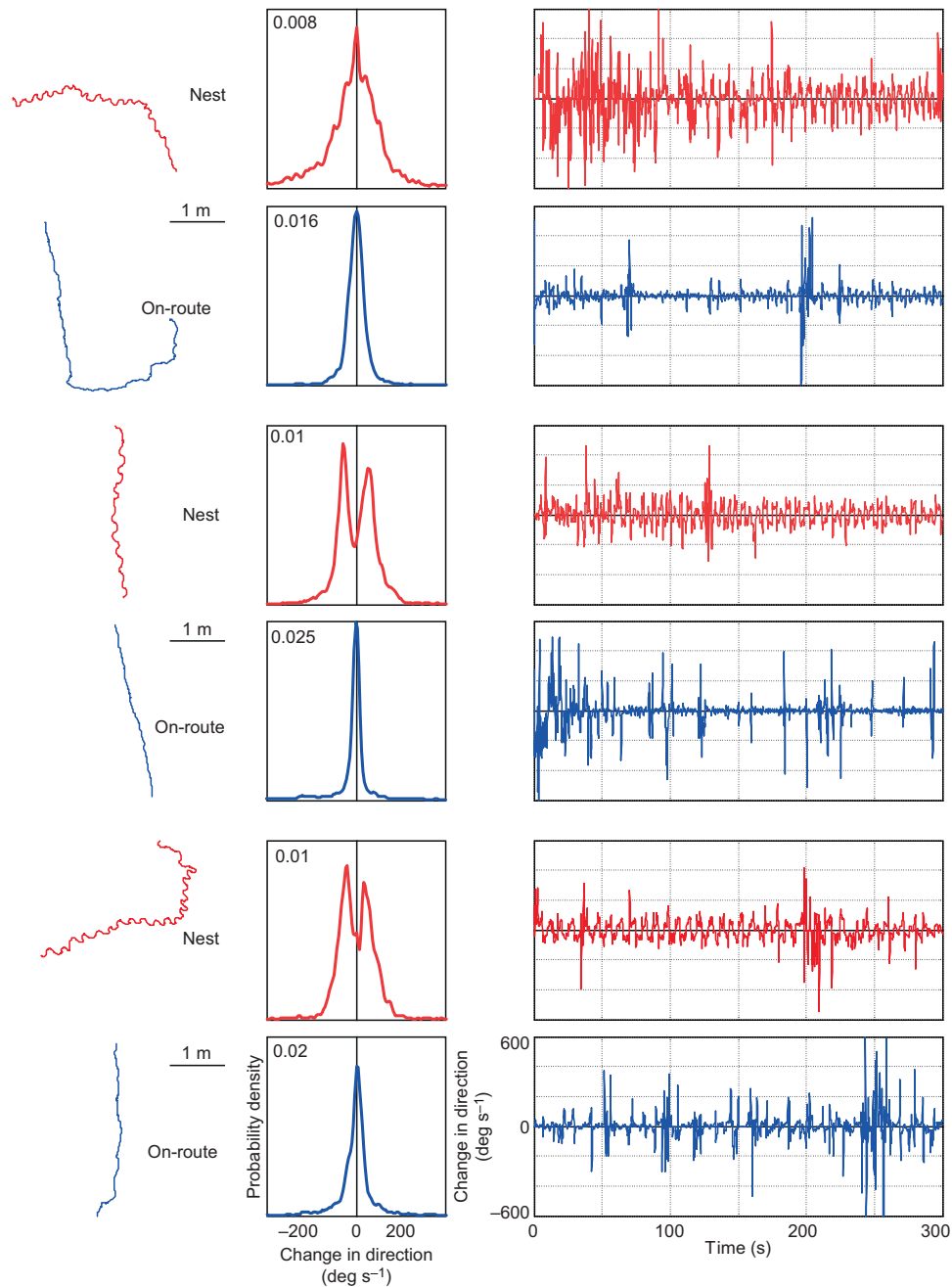


Fig. 4. Ants walk differently at the nest and the on-route location. Shown are path segments (left), the distribution of changes in walking direction during the first 5 min (middle) and the time series of changes in walking direction over 5 min (right) for three ants (top, centre, bottom), each recorded at the nest (red) and at the on-route location (blue). Changes in walking direction were determined at 11 frames s⁻¹ to reduce measurement noise. See Fig. S3 for auto-correlation functions.

route, several metres away from the nest, ants can recover the goal direction without the need to physically move and sample neighbouring locations. Second, we found no evidence that they 'expect' outcomes from their behaviour, such as a changing visual

scene or increasing certainty about the location of the nest. *Myrmecia croslandi* ants showed no evidence of monitoring the distance that separates them from the goal, unlike for instance ants that rely strongly on path integration (Dahmen et al., 2017). Third,

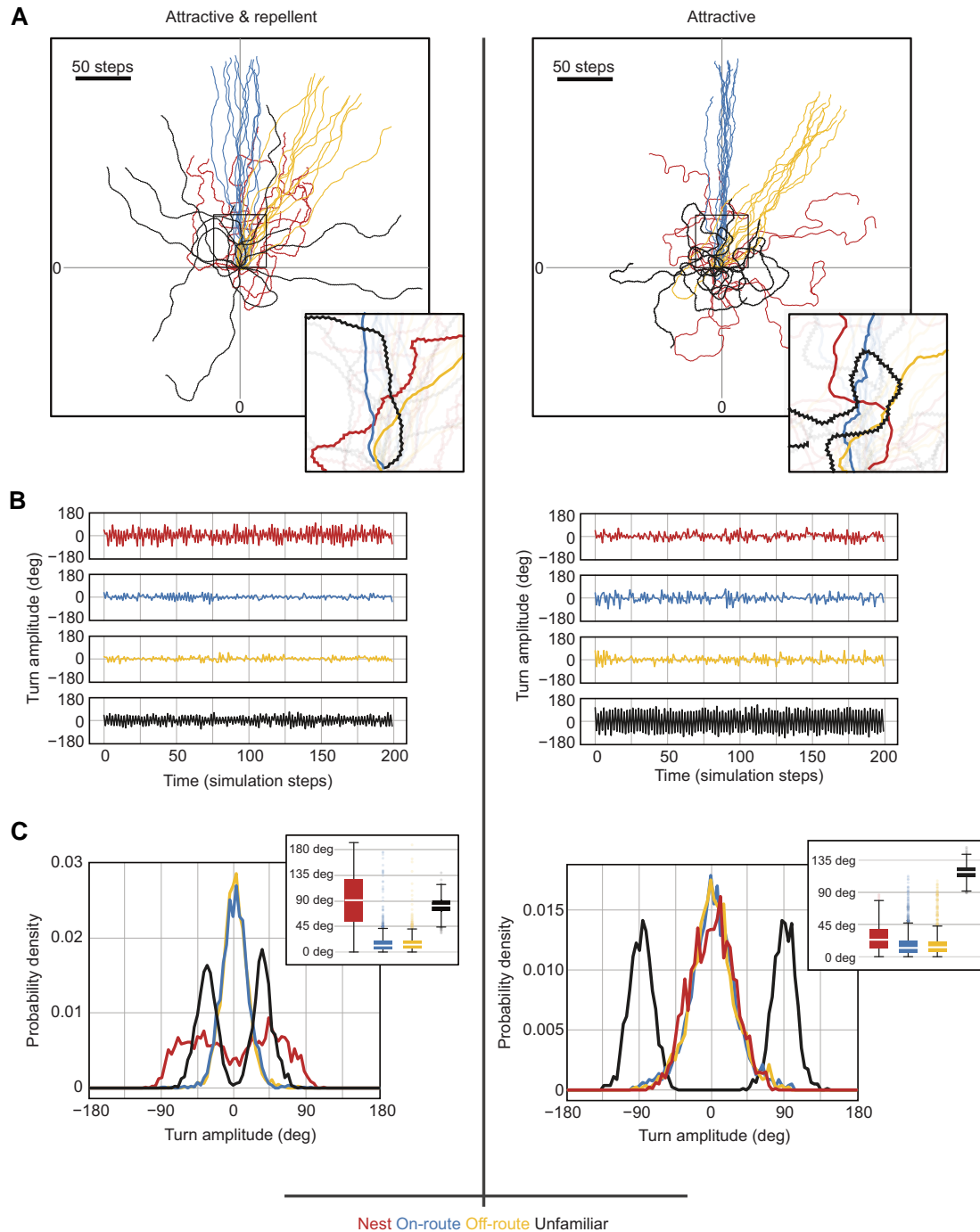


Fig. 5. Results of agent-based visual navigation using both attractive and repellent views (left) and attractive views only (right). We simulated 10 agents walking 200 steps at each nest (red), on-route (blue), off-route (yellow) and unfamiliar (black) release locations. (A) Resulting paths. Insets show close-up details of example paths. (B) Turn amplitudes over time (simulation steps) for one example at each of the release locations. (C) Probability density of turn amplitudes at the four release locations. Insets show box and whisker plots for the same distributions.

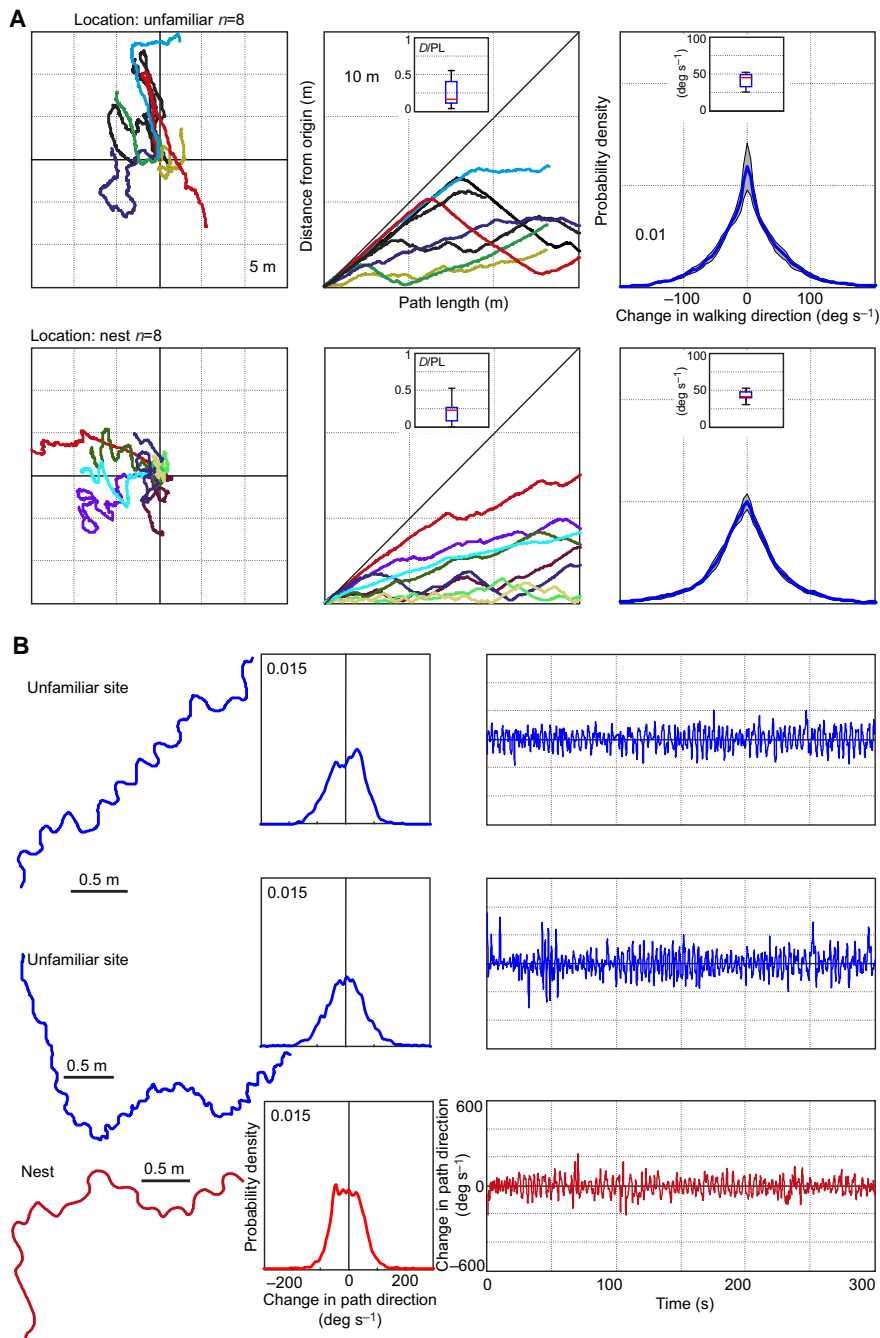


Fig. 6. Ants behave in a similar way at a completely unfamiliar location and at the nest. (A) Top: paths (left), distance from start over path length (middle) and probability density of changes in walking direction (right) for 8 tethered ants at a completely unfamiliar location. Bottom: as for A, for 8 ants at the nest location. Insets in middle panels show boxplots of final distance to path length ratios after 5 min, which are not different between the unfamiliar and the nest location (Wilcoxon rank sum test unfamiliar versus nest location: $P=0.7984$, ranksum=71). Insets in right panels show the boxplots of mean absolute values of changes in path direction over 5 min, which are not different between the unfamiliar and the nest location (Wilcoxon rank sum test unfamiliar versus nest location: $P=0.9591$, ranksum=67). (B) Example paths (left), probability density of changes in path direction (middle) and time series of changes in path direction (right) for two ants at the unfamiliar site (blue) and one ant over the nest (red).

ants behave differently when positioned above the nest, by following random heading directions and frequently changing their walking direction. These are the characteristics of search behaviour and thus could be interpreted as indicating that ants ‘know’ that they are at the nest, as if they possessed location information. However, our simulation results demonstrate that the

nest-specific behaviour of ants can be parsimoniously explained by the density of attractive, nest-directed, and repellent views away from the nest that at least *M. croslandi* ants are likely to acquire in the course of systematic scanning movements during their learning walks (e.g. Jayatilaka et al., 2018). Our simulation also confirms that the same parsimonious mechanism can recover a correct direction

from on- and off-route locations, as previous modelling has indicated (Baddeley et al., 2011, 2012; Narendra et al., 2013; Wystrach et al., 2013a; Kodzhabashev and Mangan, 2015).

Alignment matching and visual memories

Current thinking holds that ants during their learning walks learn nest-directed views (*Cataglyphis* sp.: Fleischmann et al., 2016, 2017, 2018a,b; *Ocymyrmex robustior*: Müller and Wehner, 2010; *Melophorus bagoti*: Wehner et al., 2004; Muser et al., 2005) and possibly both nest-directed views and views pointing away from the nest (*M. croslandi*: Jayatilaka et al., 2018; Zeil and Fleischmann, 2019). In addition, they memorize the views they experience along routes as they go back and forth on foraging excursions (Wehner et al., 1996; Mangan and Webb, 2012; Kohler and Wehner, 2005; Wystrach et al., 2011b; Freas and Spetch, 2019).

When using their visual memories to navigate, the currently perceived panorama provides a heading direction if the comparison between memorized views and the current view generates a detectable minimum of the rotational image difference function (see Narendra et al., 2013). This is a basic measure of familiarity and at any location, the direction presenting the most familiar view would provide the deepest (lowest) minimum. At both the on-route and off-route location, ants on the trackball were free to scan the panorama and detect the direction of any present minima. Our results show that they were successfully able to recover the goal direction by doing so (Fig. 2). On route, some ants headed to the nest while others aimed at their foraging trees, reflecting their motivation to home or to forage.

While the directedness of ants at the on-route site would have been supported by both learning walk views and views learnt along the route, their directedness at the off-route (west) location depends on their detecting a higher similarity with learning walk views directed at the nest from the west compared with all other nest-directed views. As shown here and before (Narendra et al., 2013; Zeil et al., 2014; Stürzl et al., 2015), this is possible up to 10–15 m distance from the nest in the open woodland habitats of *M. croslandi* ants, provided ants have acquired such nest-directed views about 1–5 m away from the nest (see Fig. 2B, right).

When released at the nest, ants behaved differently. They walked in various directions and displayed larger turns that regularly alternated between left and right, resulting in sinusoidal paths. So are nest views special?

As far as navigational information is concerned, the situation at the nest is indeed different compared with that for both on- and off-route sites. During their learning walks, ants will have encountered a dense set of views at different distances and compass bearings around the nest, each potentially tagged with the nest direction through path integration (Müller and Wehner, 2010; Graham et al., 2010; Baddeley et al., 2012; Fleischmann et al., 2018a; Jayatilaka et al., 2018; Zeil and Fleischmann, 2019). In contrast to other locations, tethered ants placed above the nest location thus will encounter attractive familiar views (or deep rotIDF minima) in many compass directions, which might explain why they initially walked in various directions at this location.

The high-amplitude oscillation displayed by ants at the nest location, however, is puzzling. Previous models suggest that experiencing a familiar (attractive) view should inhibit turns and favour forward motion (Zeil, 2012; Möller, 2012; Baddeley et al., 2011, 2012; Wystrach et al., 2013a; Kodzhabashev and Mangan, 2015; Ardin et al., 2016), which is clearly not the case here. The behaviour of tethered ants on top of the nest can be interpreted as a search for the nest entrance, which in ants relying on path integration

is characterized by frequent changes in path direction and a systematic pattern of increasing loops around the expected location of the goal (e.g. Schultheiss et al., 2015). To our knowledge, however, no analysis of the fine-scale changes in orientation of searching ants – as we observed them here – has been done to date.

Previous work has suggested that the recognition of views memorized at the nest may trigger specific behaviours when the ant is subsequently released in unfamiliar locations (Wystrach et al., 2013b). This interpretation may suggest positional knowledge, or at least that views close to the nest are categorized separately from route views during learning and being treated differently when recognized. In the following, we discuss the results of our simulation that suggest a parsimonious and unifying explanation for view-based route guidance, pinpointing goals and the current observation of high-amplitude oscillation at the nest without the need to invoke positional knowledge or the need for a ‘trigger’ of search behaviour. Our agent-based modelling exhibits the same pattern of fine-scale oscillations, including overall changes in path direction, but only if we assume that the agent operates with both attractive and repellent memory banks.

Continuously integrating attractive and repellent views

Our model was developed quite independently (Le Moël and Wystrach, 2019 preprint) to explain other recently observed phenomena, such as how ants manage to use views for guidance while walking backward and thus facing in the anti-nest direction (Schwarz et al., 2019 preprint); or how ants learn to detour areas along their route associated with an aversive experience (Wystrach et al., 2019b preprint). Interestingly, this new model happens to also capture the current results remarkably well. The model is based on two assumptions: (1) that ants store both attractive and repellent views during their learning walks, as suggested by Jayatilaka et al. (2018), and (2) that guidance involves an oscillator resulting in a continuous alternation between left and right turns (Namiki and Kanzaki, 2016; Kodzhabashev and Mangan, 2015; Wystrach et al., 2016). The model assumes no positional knowledge whatsoever, only procedural knowledge.

Several pieces of evidence suggest that insects possess an intrinsic oscillator triggering alternatively left and right body rotations, the amplitude of which can be modulated by the stimuli perceived (Namiki and Kanzaki, 2016; Lent et al., 2013; Wystrach et al., 2016). Such a control of oscillations can provide guidance along odour plumes (Namiki and Kanzaki, 2016) and odour gradients (Wystrach et al., 2016), supports visual route following (Kodzhabashev and Mangan, 2015) and greatly facilitates the integration of different sources of stimulation (Wystrach et al., 2016). In the case of visual route following, the amplitude of the oscillations needs to be modulated by the familiarity of the currently perceived view. The suggestion is that familiar views trigger small turns whereas unfamiliar views trigger large turns, and that the direction of the turn is dependent on the current state of the oscillator. Because views are assumed to be memorized while moving along the route, during route recapitulation, visual familiarity is higher when facing in the correct route direction. This model is sufficient for an agent to recapitulate a route in naturalistic environments (Kodzhabashev and Mangan, 2015). However, when released at the nest, this model does not predict large-amplitude oscillations such as the ones we observed here in ants. On the contrary, because of the high familiarity experienced at the nest, which results from the collection of nest-oriented views acquired during learning walks, the model predicts an inhibition of the oscillations whatever the current facing direction (see Fig. 5, right).

The visual memories used by insect navigators are probably stored in the mushroom bodies (Webb and Wystrach, 2016), but current models assume only the existence of attractive memories (Möller, 2012; Baddeley et al., 2011; 2012; Wystrach et al., 2013a; Kodzhabashev and Mangan, 2015; Ardin et al., 2016). Here, we incorporated into the model the recent suggestion that ants store both attractive and repellent views, mimicking the so-called appetitive/aversive output pathways from the insect mushroom bodies (e.g. Oswald et al., 2015; Saumweber et al., 2018) (Fig. 1D). Indeed, during their learning walks, many ants, not only *M. croslandi* (Jayatilaka et al., 2018), display regular head and body oscillations, facing alternatively towards and away from the nest (Zeil and Fleischmann, 2019). We assumed in our model that these views form two distinct memory banks – one holding attractive, nest-directed, views and one holding repellent views pointing away from the nest – and that the two sets are used continuously and simultaneously during homing. Our agent compares the current view with both sets of memories at each time step and thus obtains two familiarity values, one for attraction (high familiarity, inhibiting turns) and one for repulsion (high familiarity, triggering large turning amplitudes). Given that both memory pathways have antagonist outcomes, they can be integrated by subtracting attractive and repellent familiarity values, resulting in what we called here an overall drive, which modulates the amplitude of the oscillator (Fig. 1C).

Interestingly, this model closely mimics ant behaviour as documented in our behavioural experiments. If released on a fictive treadmill (preventing the agent from translating), it displays high-amplitude turns when released on top of the nest, and much lower amplitude turns when released further along the homing route. In contrast, when using the attractive memory bank only, the agent produces low-amplitude turns at the nest (Fig. 5).

The behaviour of the agent when combining attractive and repellent views is straightforward to explain (Fig. 1C). At the route release point, facing in the correct direction, the simulation generates very small turns because only the attractive memory bank provides a good match. By integrating this with a high unfamiliarity of the repellent memory bank, we obtain a very low overall drive, and thus small turns. However, when released at the nest, whatever the direction the agent faces, there are always both attractive and repellent views that are matching the current view (Fig. 1C), the reason being that these views, when acquired during learning walks, are experienced in multiple compass directions at very closely spaced locations (Fig. 1B). Both attractive and repellent pathways signal high familiarity values and cancel each other out, resulting in large turns.

Testing the model's prediction

Interestingly, the attractive/repellent memory bank model makes a rather counterintuitive prediction, because it relies on the relative difference in familiarity between attractive and repellent pathways and not on the absolute familiarity experienced: the agent's behaviour should be similar when on top of the nest and at a completely unfamiliar location, outside the catchment area of acquired views. At the nest, both attractive and repellent memories result in high familiarity, so their signals cancel each other when integrated (attractive–repellent), resulting in large turns. In completely unfamiliar terrain, both attractive and repellent memories result in very low familiarity, and thus their signals equally cancel each other when integrated (attractive–repellent), also resulting in large turns (Fig. 1C).

As predicted by the model, our experiments indeed showed that ants tethered at a completely unfamiliar location exhibited a very

similar behaviour to that when released on top of the nest: that is, they displayed regular high-amplitude path oscillations (Fig. 6).

Integration with path integration

We did not incorporate integration of path integration information and landmark panorama guidance in our model and so do not at this stage tackle the fact that FV ants (i.e. those captured with a remaining path integration home vector) showed a small bias towards the home vector direction at the nest location (Figs 2 and 3, FV versus ZV ants). In *M. croslandi* foragers, as in other ants, path integration information and scene information are integrated (Collett et al., 2001; Collett, 2012; Reid et al., 2011; Legge et al., 2014; Narendra et al., 2013; Wystrach et al., 2015; Wehner et al., 2016), with familiar views more strongly weighted – to the degree that a current view providing information on heading direction can completely override conflicting information from path integration (Kohler and Wehner, 2005; Narendra et al., 2013; Zeil et al., 2014). In ants that rely heavily on path integration, this information is more strongly weighted as the length of the vector increases (Wystrach et al., 2015; Wystrach et al., 2019a). The bias towards the home vector direction observed here in FV ants fits this current view, which is summarized in a recent model (Hoinville and Wehner, 2018). Also, experienced ants seem to rely less on path integration than naive ants, and rather display a search when on unfamiliar terrain (Schwarz et al., 2017a), which may explain why path integration information is never strongly weighted in the long-lived *M. croslandi*.

Outlook

Our results may contribute to the lingering debate about the format of spatial knowledge underlying visual navigation in insects and animals in general (e.g. Cheeseman et al., 2014a,b; Cheung et al., 2014; Warren, 2019). We showed that ants released on top of the nest displayed large turns. These results are clearly at odds with the current procedural models, stipulating that the high familiarity of views at the nest should inhibit turns. In contrast, the ants' behaviour suggested that they could derive positional knowledge from the current views, given the interpretation that the ants searched because they recognized that they were at the nest. Previous results, such as the apparent ability of insects to make shortcuts, also favoured explanations assuming positional rather than procedural knowledge (e.g. Cheeseman et al., 2014a,b; Warren, 2019). However, as often in the insect literature (Cartwright and Collett, 1987; Collett et al., 2007; Cruse and Wehner, 2011; Wystrach and Graham, 2012; Narendra et al., 2013; Cheung et al., 2014), an alternative, more parsimonious explanation can also explain our results: ants may simply combine attractive and repellent memories. Importantly, this procedural explanation did not come from actively seeking for it, but emerged from other observations, such as the way in which ants behave when learning views around the nest (Jayatilaka et al., 2018), how they avoid adverse situations (Wystrach et al., 2019b preprint), how they steer while walking backwards (Schwarz et al., 2017b; Schwarz et al., 2019 preprint), as well as how appetitive and aversive memory pathways are combined in other insects such as flies (Felsenberg et al., 2018) and fly larvae (Eichler et al., 2017).

Our simulation made the unexpected prediction that behaviour in completely unfamiliar terrain should be the same as at the very familiar nest, which we confirmed by subsequent experimentation. Purely scene familiarity-based modelling replicates these results with astonishing detail, providing support for the suggestion that ants during their learning walks acquire both attractive, nest-directed

views and repellent views when pointing away from the nest during systematic scanning movements (Jayatilaka et al., 2018; Zeil and Fleischmann, 2019). It is not clear at present, however, whether all views are memorized irrespective of gaze direction or only when the ants' head is aligned parallel to the home vector (see discussion in Jayatilaka et al., 2018). We show here, at least, that the distinctly different behaviour of ants over the nest location can be replicated if an agent has an attractive and a repellent scene memory bank.

The most parsimonious explanation for our observations is therefore that the ants operate on procedural rather than location information (*sensu* Collett et al., 2002; Wehner et al., 2006; Graham and Philippides, 2017): at both familiar and unfamiliar locations away from the nest they may know where to go, but they do not know where they are. Moreover, the main assumptions of our simulation – attractive and repellent view comparison driving an oscillator – can be tested by a detailed comparison of the gaze and path directions of individually identified ants during their learning walks and during their subsequent approach to the nest, when returning from foraging excursions. Such an analysis may also reveal how ants eventually pinpoint the nest entrance, which none of the current homing models can properly explain.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.M., Z.K., A.N., A.W., J.Z.; Methodology: T.M., Z.K., H.D., A.N., F.L., A.W., J.Z.; Software: T.M., Z.K., H.D., F.L., A.W., J.Z.; Validation: T.M., Z.K., J.Z.; Formal analysis: T.M., Z.K., F.L., A.W., J.Z.; Investigation: T.M., Z.K., A.N., F.L., A.W., J.Z.; Resources: J.Z.; Writing - original draft: T.M., A.W., J.Z.; Writing - review & editing: T.M., Z.K., H.D., A.N., A.W., J.Z.; Visualization: T.M., A.W., J.Z.; Supervision: J.Z.; Project administration: J.Z.; Funding acquisition: A.N., J.Z.

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Supplementary information

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References

- Ardin, P., Peng, F., Mangan, M., Lagogiannis, K. and Webb, B. (2016). Using an insect mushroom body circuit to encode route memory in complex natural environments. *PLoS Comp. Biol.* **12**, e1004683. doi:10.1371/journal.pcbi.1004683
- Baddeley, B., Graham, P., Philippides, A. and Husbands, P. (2011). Holistic visual encoding of ant-like routes: navigation without waypoints. *Adaptive Behav.* **19**, 3–15. doi:10.1177/1059712310395410
- Baddeley, B., Graham, P., Husbands, P. and Philippides, A. (2012). A model of ant route navigation driven by scene familiarity. *PLoS Comp. Biol.* **8**, e1002336. doi:10.1371/journal.pcbi.1002336
- Cartwright, B.A. and Collett, T.S. (1987). Landmark maps for honeybees. *Biol. Cybernet.* **57**, 85–93. doi:10.1007/BF00318718
- Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D. M., Gallistel, C. R., Warman, G. R. and Menzel, R. (2014a). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *Proc. Natl Acad. Sci. USA* **111**, 8949–8954. doi:10.1073/pnas.1408039111
- Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D. M., Gallistel, C. R., Warman, G. R. and Menzel, R. (2014b). Reply to Cheung et al.: the cognitive map hypothesis remains the best interpretation of the data in honeybee navigation. *Proc. Natl Acad. Sci. USA* **111**, E4398. doi:10.1073/pnas.1415738111
- Cheung, A., Collett, M., Collett, T. S., Dewar, A., Dyer, F. C., Graham, P., Mangan, M., Narendra, A., Philippides, A., Stürzl, W. et al. (2014). Still no convincing evidence for cognitive map use by honeybees. *Proc. Natl Acad. Sci. USA* **111**, E4396–E4397. doi:10.1073/pnas.1413581111
- Collett, M. (2012). How navigational guidance systems are combined in a desert ant. *Curr. Biol.* **22**, 927–932. doi:10.1016/j.cub.2012.03.049
- Collett, T.S., and Zeil, J. (2018). Insect learning flights and walks. *Curr. Biol.* **28**, R984–R988. doi:10.1016/j.cub.2018.04.050
- Collett, T. S., Collett, M. and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204**, 1635–1639.
- Collett, M., Harland, D. and Collett, M. (2002). The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees. *J. Exp. Biol.* **205**, 807–814.
- Collett, T. S., Graham, P. and Harris, R. A. (2007). Novel landmark-guided routes in ants. *J. Exp. Biol.* **210**, 2025–2032. doi:10.1242/jeb.000315
- Collett, M., Chittka, L. and Collett, T. S. (2013). Spatial memory in insect navigation. *Curr. Biol.* **23**, R789–R800. doi:10.1016/j.cub.2013.07.020
- Cruse, H. and Wehner, R. (2011). No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comp. Biol.* **7**, e1002009. doi:10.1371/journal.pcbi.1002009
- Dahmen, H. J., Wahl, V. L., Pfeffer, S. E., Mallot, H. A. and Wittlinger, M. (2017). Naturalistic path integration of *Cataglyphis* desert ants on an air-cushioned lightweight spherical treadmill. *J. Exp. Biol.* **220**, 634–644. doi:10.1242/jeb.148213
- Eichler, K., Li, F., Litwin-Kumar, A., Park, Y., Andrade, I., Schneider-Mizell, C. M., Saumweber, T., Huser, A., Eschbach, C., Gerber, B. et al. (2017). The complete connectome of a learning and memory centre in an insect brain. *Nature* **548**, 175–182. doi:10.1038/nature23455
- Felsenberg, J., Jacob, P. F., Walker, T., Barnstedt, O., Edmondson-Stait, A. J., Pleijzier, M. W., Otto, N., Schlegel, P., Sharifi, N., Perisse, E. et al. (2018). Integration of parallel opposing memories underlies memory extinction. *Cell* **175**, 709–722.e15. doi:10.1016/j.cell.2018.08.021
- Fleischmann, P. N., Christian, M., Müller, V. L., Rössler, W. and Wehner, R. (2016). Ontogeny of learning walks and the acquisition of landmark information in desert ants *Cataglyphis fortis*. *J. Exp. Biol.* **219**, 3137–3145. doi:10.1242/jeb.140459
- Fleischmann, P. N., Grob, R., Wehner, R. and Rössler, W. (2017). Species-specific differences in the fine structure of learning walk elements in *Cataglyphis* ants. *J. Exp. Biol.* **220**, 2426–2435. doi:10.1242/jeb.158147
- Fleischmann, P. N., Grob, R., Müller, V. L., Wehner, R. and Rössler, W. (2018a). The geomagnetic field is a compass cue in *Cataglyphis* ant navigation. *Curr. Biol.* **28**, 1440–1444. doi:10.1016/j.cub.2018.03.043
- Fleischmann, P. N., Rössler, W. and Wehner, R. (2018b). Early foraging life: spatial and temporal aspects of landmark learning in the ant *Cataglyphis noda*. *J. Comp. Physiol. A* **204**, 579–592. doi:10.1007/s00359-018-1260-6
- Freas, C. A. and Spetch, M. L. (2019). Terrestrial cue learning and retention during the outbound and inbound foraging trip in the desert ant, *Cataglyphis velox*. *J. Comp. Physiol. A* **205**, 177–189. doi:10.1007/s00359-019-01316-6
- Graham, P. and Cheng, K. (2009). Ants use the panoramic skyline as a visual cue during navigation. *Curr. Biol.* **19**, R935–R937. doi:10.1016/j.cub.2009.08.015
- Graham, P. and Philippides, A. (2017). Vision for navigation: what can we learn from ants? *Arthropod Struct. Dev.* **46**, 718–722. doi:10.1016/j.asd.2017.07.001
- Graham, P., Philippides, A. and Baddeley, B. (2010). Animal cognition: multimodal interactions in ant learning. *Curr. Biol.* **20**, R639–R640. doi:10.1016/j.cub.2010.06.018
- Hoinville, T. and Wehner, R. (2018). Optimal multiguide integration in insect navigation. *Proc. Natl. Acad. Sci. USA* **115**, 2824–2829. doi:10.1073/pnas.1721668115
- Jayatilaka, P., Narendra, A., Reid, F. S., Cooper, P. and Zeil, J. (2011). Different effects of temperature on foraging activity schedules in sympatric *Myrmecia* ants. *J. Exp. Biol.* **214**, 2730–2738. doi:10.1242/jeb.053710
- Jayatilaka, P., Raderschall, A. C., Narendra, A. and Zeil, J. (2014). Individual foraging patterns of the jack jumper ant *Myrmecia croslandi* (Hymenoptera: Formicidae). *Myrmecol. News* **19**, 75–83. doi:10.1242/jeb.185306
- Jayatilaka, P., Murray, T., Narendra, A. and Zeil, J. (2018). The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*. *J. Exp. Biol.* **221**, jeb185306. doi:10.1242/jeb.185306
- Kodzhabashev, A. and Mangan, M. (2015). Route following without scanning. In *Biomimetic and Biohybrid Systems* (ed. S.P. Wilson, P.F.M.J. Verschueren, A. Mura and T.J. Prescott), pp. 199–210. Lecture Notes in Artificial Intelligence 9222. Heidelberg, Berlin, New York: Springer Verlag.
- Kohler, M. and Wehner, R. (2005). Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors? *Neurobiol. Learn. Memory* **83**, 1–12. doi:10.1016/j.nlm.2004.05.011
- Legge, E.L.G., Wystrach, A., Spetch, M.L. and Cheng, K. (2014). Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues. *J. Exp. Biol.* **217**, 4159–4166. doi:10.1242/jeb.107862
- Lent, D.D., Graham, P. and Collett, T.S. (2013). Visual scene perception in navigating wood ants. *Curr. Biol.* **23**, 684–690. doi:10.1016/j.cub.2013.03.016

- Le Möel, F. and Wystrach, A.** (2019). Opponent processes in visual memories: a model of attraction and repulsion in navigating insects' mushroom bodies. *bioRxiv*, 877449. doi:https://doi.org/10.1101/2019.12.16.877449
- Mangan, M. and Webb, B.** (2012). Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*). *Behav. Ecol.* **23**, 944-954. doi:10.1093/beheco/ars051
- Möller, R.** (2012). A model of ant navigation based on visual prediction. *J. Theo. Biol.* **305**, 118-130. doi:10.1016/j.jtbi.2012.04.022
- Müller, M. and Wehner, R.** (2010). Path integration provides a scaffold for landmark learning in desert ants. *Curr. Biol.* **20**, 1368-1371. doi:10.1016/j.cub.2010.06.035
- Muser, B., Sommer, S., Wolf, H. and Wehner, R.** (2005). Foraging ecology of the thermophilic Australian desert ant *Melophorus bagoti*. *Austr. J. Zool.* **53**, 301-311. doi:10.1071/ZO05023
- Namiki, S. and Kanzaki, R.** (2016). The neurobiological basis of orientation in insects: insights from the silkworm mating dance. *Curr. Opin. Insect Sci.* **15**, 16-26. doi:10.1016/j.cois.2016.02.009
- Narendra, A., Gourmaud, S. and Zeil, J.** (2013). Mapping the navigational knowledge of individually foraging ants *Myrmecia croslandi*. *Proc. R. Soc. Lond. B* **280**, 20130683. doi:10.1098/rspb.2013.0683
- Owald, D., Felsenberg, J., Talbot, C. B., Das, G., Perisse, E., Huetteroth, W. and Waddell, S.** (2015). Activity of Defined Mushroom Body output neurons underlies learned olfactory behavior in *Drosophila*. *Neuron* **86**, 417-427. doi:10.1016/j.neuron.2015.03.025
- Philippides, A., Baddeley, B., Cheng, K. and Graham, P.** (2011). How might ants use panoramic views for route navigation? *J. Exp. Biol.* **214**, 445-451. doi:10.1242/jeb.046755
- Reid, S.F., Narendra, A., Hemmi, J.M. and Zeil, J.** (2011). Polarised skylight and the landmark panorama provide night active bull ants with compass information during route following. *J. Exp. Biol.* **214**, 363-370. doi:10.1242/jeb.049338
- Saumweber, T., Rohwedder, A., Schleyer, M., Eichler, K., Chen, Y.-C., Aso, Y., Cardona, A., Eschbach, C., Kobler, O., Voigt, A. et al.** (2018). Functional architecture of reward learning in mushroom body extrinsic neurons of larval *Drosophila*. *Nature Comm.* **9**, 1104. doi:10.1038/s41467-018-03130-1
- Schultheiss, P., Cheng, K. and Reynold, A. M.** (2015). Searching behavior in social Hymenoptera. *Learn. Motiv.* **50**, 59-67. doi:10.1016/j.lmot.2014.11.002
- Schwarz, S., Clement, L., Gkaniats, E. and Wystrach, A.** (2019). How do backward walking ants (*Cataglyphis velox*) cope with navigational uncertainty? *bioRxiv* doi:https://doi.org/10.1101/2019.12.16.877704
- Schwarz, S., Wystrach, A. and Cheng, K.** (2017a). Ants' navigation in an unfamiliar environment is influenced by their experience of a familiar route. *Sci. Rep.* **7**, 14161. doi:10.1038/s41598-017-14036-1
- Schwarz, S., Mangan, M., Zeil, J., Webb, B. and Wystrach, A.** (2017b). How ants use vision when homing backward. *Curr. Biol.* **27**, 401-407. doi:10.1016/j.cub.2016.12.019
- Stürzl, W., Grix, I., Mair, E., Narendra, A. and Zeil, J.** (2015). Three-dimensional models of natural environments and the mapping of navigational information. *J. Comp. Physiol. A* **201**, 563-584. doi:10.1007/s00359-015-1002-y
- Warren, W. H.** (2019). Non-Euclidean navigation. *J. Exp. Biol.* **222**, jeb187971. doi:10.1242/jeb.187971
- Webb, B. and Wystrach, A.** (2016). Neural mechanisms of insect navigation. *Curr Opin. Insect sci.* **15**, 27-39. doi:10.1016/j.cois.2016.02.011
- Wehner, R., Michel, B. and Antonsen, P.** (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.
- Wehner, R., Meier, C. and Zollikofer, C.** (2004). The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* **29**, 240-250. doi:10.1111/j.0307-6946.2004.00591.x
- Wehner, R., Boyer, M., Loertscher, F., Sommer, S. and Menzi, U.** (2006). Ant navigation: one-way routes rather than maps. *Curr. Biol.* **16**, 75-79. doi:10.1016/j.cub.2005.11.035
- Wehner, R., Hoinville, T., Cruse, H., and Cheng, K.** (2016). Steering intermediate courses: desert ants combine information from various navigational routines. *J. Comp. Physiol. A* **202**, 459-472. doi:10.1007/s00359-016-1094-z. Epub 2016 Jun 3.
- Wystrach, A. and Graham, P.** (2012). What can we learn from studies of insect navigation? *Anim. Behav.* **84**, 13-20. doi:10.1016/j.anbehav.2012.04.017
- Wystrach, A., Beugnon, G. and Cheng, K.** (2011a). Landmarks or panoramas: what do navigating ants attend to for guidance? *Front. Zool.* **8**, 21. doi:10.1186/1742-9994-8-21
- Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G. and Cheng, K.** (2011b). Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *J. Comp. Physiol. A* **197**, 167-179. doi:10.1007/s00359-010-0597-2
- Wystrach, A., Beugnon, G. and Cheng, K.** (2012). Ants might use different view-matching strategies on and off the route. *J. Exp. Biol.* **215**, 44-55. doi:10.1242/jeb.059584
- Wystrach, A., Mangan, M., Philippides, A. and Graham, P.** (2013a). Snapshots in ants? New interpretations of paradigmatic experiments. *J. Exp. Biol.* **216**, 1766-1770. doi:10.1242/jeb.082941
- Wystrach, A., Schwarz, S., Baniel, A. and Cheng, K.** (2013b). Backtracking behaviour in lost ants: an additional strategy in their navigational toolkit. *Proc. Roy. Soc. B* **280**, 20131677. doi:10.1098/rspb.2013.1677
- Wystrach, A., Lagogiannis, K. and Webb, B.** (2016). Continuous lateral oscillations as a core mechanism for taxis in *Drosophila* larvae. *Elife* **5**, e15504. doi:10.7554/eLife.15504
- Wystrach, A., Schwarz, S., Graham, P. and Cheng, K.** (2019a). Running paths to nowhere: repetition of routes shows how navigating ants modulate online the weights accorded to cues. *Anim. Cogn.* **22**, 213-222. doi:10.1007/s10071-019-01236-7
- Wystrach, A., Buehlmann, C., Schwarz, S., Cheng, K. and Graham, P.** (2019b). Avoiding pitfalls: trace conditioning and rapid aversive learning during route navigation in desert ants. *bioRxiv* 771204. doi:10.1101/771204
- Zeil, J.** (2012). Visual homing: an insect perspective. *Curr. Opin. Neurobiol.* **22**, 85-93. doi:10.1016/j.conb.2011.12.008
- Zeil, J. and Fleischmann, P.** (2019). The learning walks of ants (Formicidae, Hymenoptera). *Myrmecol. News* **29**, 93-110. doi:10.25849/myrmecol.news_029:093
- Zeil, J., Hofmann, M. I. and Chahl, J. S.** (2003). Catchment areas of panoramic snapshots in outdoor scenes. *J. Opt. Soc. Am. A* **20**, 450-469. doi:10.1364/JOSAA.20.000450
- Zeil, J., Narendra, A. and Stürzl, W.** (2014). Looking and homing: how displaced ants decide where to go. *Phil. Trans. Roy. Soc. B* **369**, 20130034. doi:10.1098/rstb.2013.0034

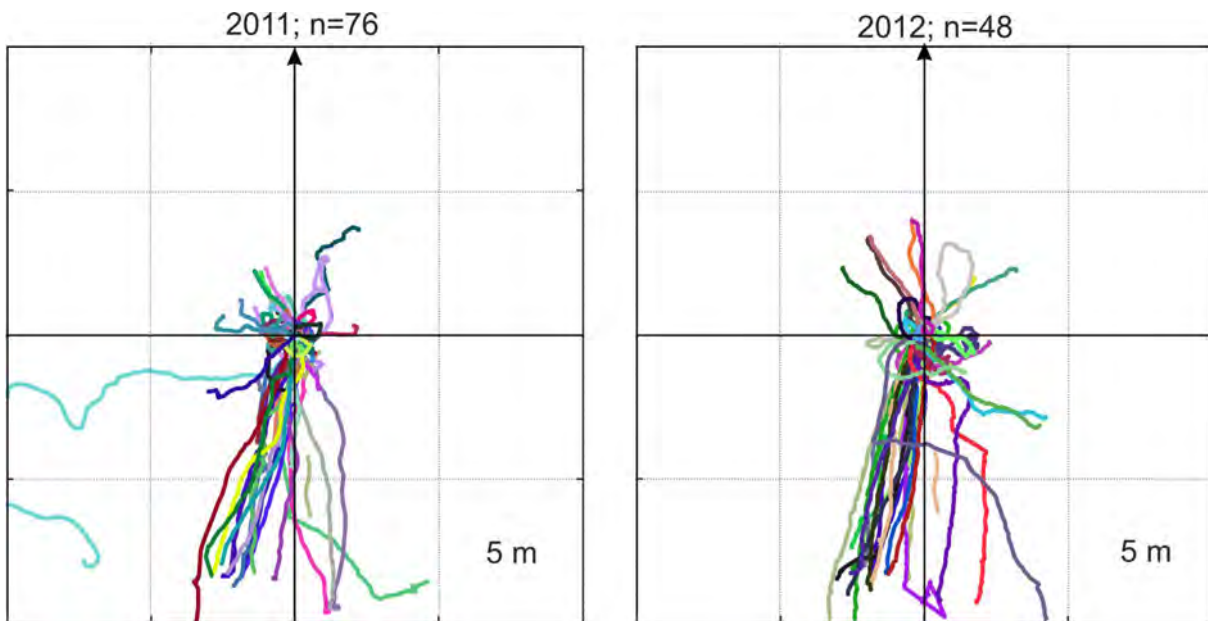
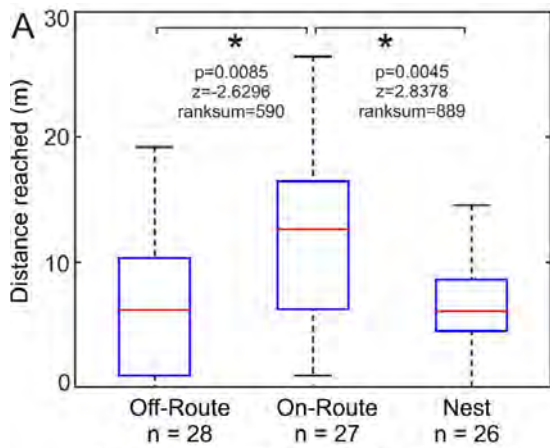
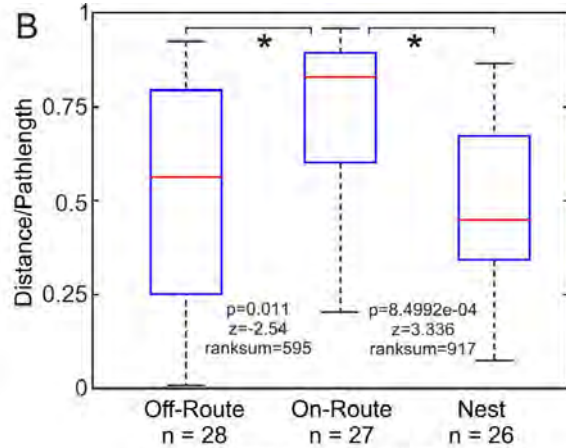


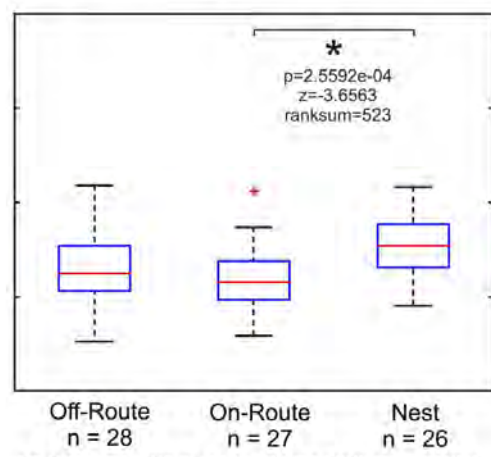
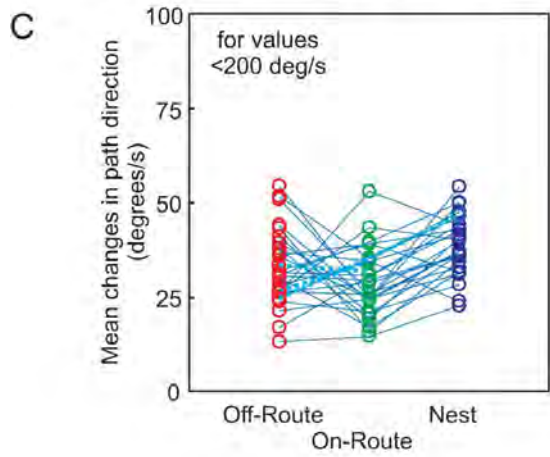
Figure S1. Foraging patterns at the *M. croslandi* nest used in this study. Panels show the individual paths of foragers as they have been recorded with differential GPS over a period of two years. These paths provided the original data for the 2D histogram shown in the middle panel of Fig. 1B.



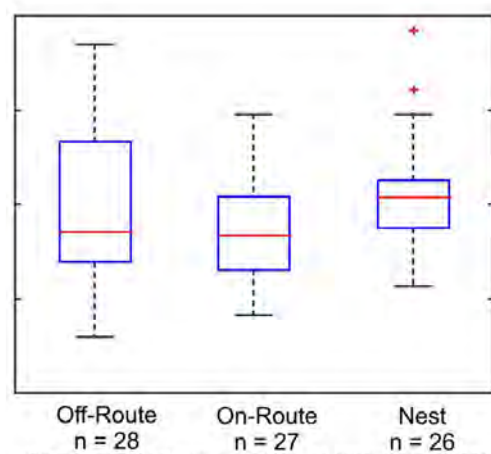
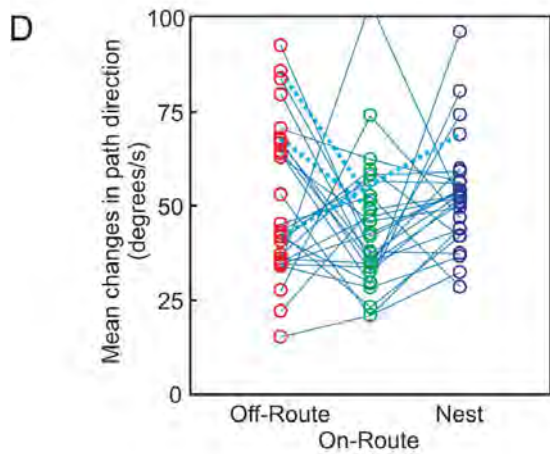
Off-Route vs Nest: $p=0.8518$; $z=0.1868$; ranksum=713



Off-Route vs Nest: $p=0.6$; $z=0.5249$; ranksum=795



Off-Route vs On-Route: $p=0.1319$; $z=1.5068$; ranksum=874
 Off-Route vs Nest: $p=0.019$; $z=-2.3458$; ranksum=634



Off-Route vs On-Route: $p=0.2097$; $z=1.2543$; ranksum=859
 Off-Route vs Nest: $p=0.4208$; $z=-0.8050$; ranksum=723
 On-Route vs Nest: $p=0.0244$; $z=-2.2507$; ranksum=602

Figure S2. Quantitative analysis of behavioural differences between Off-route, On-route and Nest locations. (A) Box plots of distances reached after 5 minutes at the three locations. Significant comparisons with a Wilcoxon Rank Sum test ($p < 0.0167$) are marked by a star and values are shown inside the panel. Values for non-significant comparisons ($p > 0.0167$) are shown below the panel. (B) Box plots of distance over path length ratios after 5 minutes at the three locations. Otherwise conventions as in (A). (C) Left panel: Individual means of the changes in path direction (absolute values $< 200^\circ/s$, determined at 11fps) for the first 5 minutes with means of individual ants connected by blue lines. Dashed lines mark cases where an ant was released at two locations only. Right panel: Boxplots of mean changes in path direction with significant differences as determined by Wilcoxon Rank Sum test marked by a star and values shown as inset. Values for non-significant comparisons are shown below the panel. (D) Same for the means and distributions of all absolute values of changes in path direction. Otherwise conventions as before.

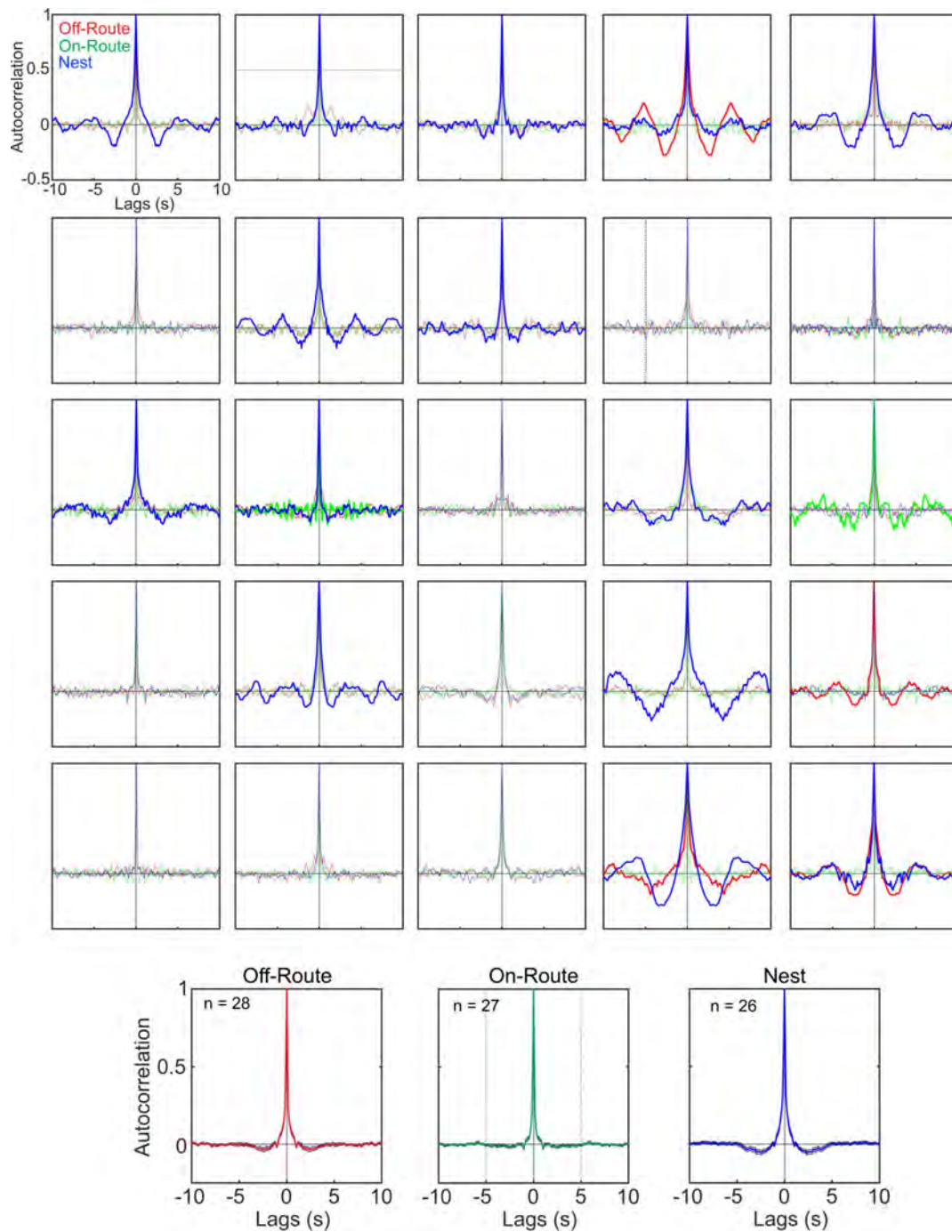


Figure S3. Comparison of auto-correlation functions of 5 minute time series of changes in path direction at the three locations. Off-route: red; On-route: green; Nest: blue for each of 25 ants that were tested at all three locations. Bottom panels show mean auto-correlations for all ants at the three locations.

Appendix B

A lateralised design for the interaction of visual memories and heading representations in navigating ants

Antoine Wystrach, Florent Le Moël, Léo Clément, Sebastian Schwarz



This appendix is available as a pre-print on **bioRxiv**.

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1 **A lateralised design for the interaction of visual memories and heading representations in**
2 **navigating ants.**

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4

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9

10 **Abstract:**

11 The navigational skills of ants, bees and wasps represent one of the most baffling examples
12 of the powers of minuscule brains. Insects store long-term memories of the visual scenes
13 they experience ¹, and they use compass cues to build a robust representation of directions
14 ^{2,3}. We know reasonably well how long-term memories are formed, in a brain area called the
15 Mushroom Bodies (MB) ⁴⁻⁸, as well as how heading representations are formed in another
16 brain area called the Central Complex (CX) ⁹⁻¹². However, how such memories and heading
17 representations interact to produce powerful navigational behaviours remains unclear ^{7,13,14}.
18 Here we combine behavioural experiments with computational modelling that is strictly
19 based on connectomic data to provide a new perspective on how navigation might be
20 orchestrated in these insects. Our results reveal a lateralised design, where signals about
21 whether to turn left or right are segregated in the left and right hemispheres, respectively.
22 Furthermore, we show that guidance is a two-stage process: the recognition of visual
23 memories – presumably in the MBs – does not directly drive the motor command, but
24 instead updates a “desired heading” – presumably in the CX – which in turn is used to
25 control guidance using celestial compass information. Overall, this circuit enables ants to
26 recognise views independently of their body orientation, and combines terrestrial and
27 celestial cues in a way that produces exceptionally robust navigation.

28

29 ***Bilaterally decorrelated input to the CX produces goal-oriented paths.***

30 We first investigated how information about the visual familiarity of the scenes – as
31 computed in the MB – could plausibly be sent to the CX for guidance given the known
32 circuitry of insect brains. Even though our current approach is an experimental one, the CX
33 circuitry is understood and conserved enough to make such effort possible using biologically
34 constrained neural modelling^{12,15–17}.

35 Recent studies have shown that the CX circuits can: 1) track the current heading, in two
36 substructures called Ellipsoid Body (EB) and Protocerebral Bridge (PB)^{10,11,18}; 2) retain a
37 desired heading representation for tens of seconds in the Fan-shaped Body (FB)¹⁴; and 3)
38 compare both current and desired headings to output compensatory left/right steering
39 commands^{14,19}. The desired heading can be updated by bilateral signals to the FB from
40 external regions¹⁴. Such a signal can plausibly come from the recognition of long-term visual
41 memories in the MB, which sends bilateral input to the FB through one relay in the Superior
42 Intermediate Protocerebrum (SIP). These observations led to the idea that navigation, such
43 as learnt route following, could emerge by having the MBs signalling to the CX when the
44 insect is facing its familiar route direction or not^{7,13,14}.

45 We thus tested the viability of this hypothesis by building a model of the CX, strictly based
46 on this connectivity (Fig. 1). Contrary to what was expected, our model shows that having
47 the bilateral ‘visual familiarity’ signals to the FB correspond with the moments when the
48 agent is facing the correct route direction did not allow straight routes to emerge. A
49 thorough search through the parameter space revealed that this configuration produces a
50 mediocre directionality at best, and is very sensitive to parameter change (Extended data fig.
51 1). Contrastingly, route following becomes extremely stable and robust to parameter
52 changes as soon as the signals to the FB from the left and right brain hemispheres
53 correspond to moments where the agent is oriented to the right or the left of its goal,
54 respectively (Fig. 1). Impressively, varying parameters (such as the time during which FB
55 neurons sustain their activity, or the heading angle away from the goal for which left or right
56 input signals are strongest) hardly has any effect: straight routes emerge as long as left and
57 right hemispheric inputs roughly correlate with a right and left heading bias, respectively
58 (Fig. 1, Extended data fig. 1). As a corollary, if left and right hemispheric inputs correlate
59 instead with left and right (rather than right and left) heading biases, a straight route in the

60 reverse direction emerges (Fig. 1). Thus, having the input signal correlate with moments
61 where the agent faces the goal direction corresponds to a zone of transition between two
62 stable regimes of route-following in opposite directions.

63 In other words, this suggests that recognising views when facing the goal may not be a good
64 solution, and instead, it shows that the CX circuitry is remarkably adapted to control a visual
65 course as long as the input signals from the visual familiarity of the scene to both
66 hemispheres are distinct, with one hemisphere signalling when the agent's heading is biased
67 towards the right and the other, towards the left. This model makes particular predictions,
68 which we next tested with behavioural experiments.

69

70 ***The recognition of familiar views triggers compensatory left or right turns.***

71 Previous studies assumed that ants memorise views while facing the goal^{20–22} and anti-goal
72^{23–25}) directions, and that they must consequently align their body in these same directions
73 to recognise a learnt view as familiar^{26–28}. On the contrary, our modelling effort suggests
74 that ants should rather recognise views based on whether the route direction stands on
75 their 'left or right' rather than 'in front or behind'. We put this idea to the test using an
76 open-loop trackball system enabling the experimenter to choose both the position and body
77 orientation of tethered ants directly in their natural environment²⁹. We trained ants along a
78 route and captured homing individuals just before they entered their nest to ensure that
79 these so-called zero-vector ants (ZV) could no longer rely on their path integration homing
80 vector³⁰. We recorded the motor response of these ants while mounted on the trackball
81 system, in the middle of their familiar route, far from the catchment area of the nest, when
82 fixed in eight different body orientations (Fig. 2a, b). Results show that, irrespective of their
83 body orientation, ants turned mostly towards the correct route direction (Fig. 2c). When the
84 body was oriented towards (0°, nest direction) or away (180°) from the route direction, ants
85 still showed a strong preference for turning on one side (to the left or to the right,
86 depending on individuals) (Fig. 2d). This was not the case when ants were tested in
87 unfamiliar surroundings (Fig. 2c, d), showing that the lateralised responses observed on the
88 familiar route was triggered by the recognition of the visual scene. This implies that ants can
89 recognise their route independently of their body orientation, and can derive whether the

90 route direction is towards their left or their right. Importantly, even when facing the route or
91 anti-route direction, recognition of familiar views appears to trigger a 'left vs. right' decision
92 rather than a 'go forward vs. turn' decision.

93

94 ***Guidance based on memorised views involves the celestial compass.***

95 We showed that the recognition of familiar views indicates whether the goal direction is
96 towards the left or right. In principle, guidance could thus be achieved by having these
97 left/right signals directly trigger the left or right motor command. An alternative would be,
98 as in our model, that such left/right signals can be used to update the 'desired heading
99 directions' in the CX, which in turn uses its own compass information to control steering (Fig.
100 1). This makes a counterintuitive prediction: if the recognition of familiar views triggers a
101 turn towards the correct side, reversing the direction of the compass representation in the
102 CX should immediately reverse the motor decision. We tested this prediction by mirroring
103 the apparent position of the sun in the sky by 180° to *Cataglyphis velox* ants tethered to our
104 trackball system. A previous study had shown that this manipulation was sufficient to shift
105 this species' compass heading representation³¹.

106 We first tethered well-trained ZV ants (i.e., captured just before entering the nest) on our
107 trackball system with their body orientation fixed perpendicularly to their familiar route
108 direction. As expected, ants in this situation turned towards the correct route direction (Fig.
109 3, left panels, natural sun), indicating that they correctly recognised familiar visual terrestrial
110 cues. When mirroring the apparent sun's position by 180°, these ants responded by turning
111 in the opposite direction within one second (Fig. 3, left panel, mirrored sun). We repeated
112 the experiment by placing such ZV ants in the same compass direction but in an unfamiliar
113 location. In this situation, the ants turned in random directions (Fig. 3, middle panels),
114 showing that the direction initially chosen by the ants on their familiar route (Fig. 3, left
115 panels) was based on the recognition of terrestrial rather than celestial cues. It however
116 remains unclear whether the sun rotation had an impact on ants in unfamiliar terrain, as
117 ants in this situation regularly alternate between left and right turns anyway²⁵. Finally, to
118 ensure that the observed effect on route was not due to an innate bias at this particular
119 location, we repeated this experiment with ants tethered at the exact same route location

120 and body orientation, but this time only with ants that were trained to an alternative
121 straight route, which was aligned with the tethered direction of the trackball (Fig. 3, right
122 panel). As expected, these ants showed no preference in turning direction at the group level,
123 although most individuals still strongly favoured one side rather than walking straight (Fig. 3
124 right panels). Interestingly, mirroring the sun significantly reversed the individual's chosen
125 direction (even though they were aligned with their goal direction) (Fig. 3c right panels).

126 Taken together these results show that guidance based on learnt views is a two-stage
127 process: the recognition of visual memories – presumably through the MBs – does not
128 directly drive the motor command, but it instead signals a desired heading – presumably
129 through the CX –, which in turn is used to control guidance using celestial compass
130 information.

131

132 ***A complex interaction between terrestrial and celestial guidance***

133 The results from above point at a complex interaction between the use of long-term
134 memory of terrestrial cues – indicating whether the goal is left or right – and the heading
135 estimate based on compass cues. To further endorse the credibility of our proposed
136 guidance system, we used our model to explore how agents navigating along their familiar
137 route would react to a sudden 135° shift of the CX current celestial compass estimate, and
138 compared their behaviour to that of real homing ZV ants tested in a similar scenario, where
139 we shifted the sun position by 135° using a mirror (Fig. 4). Impressively, and despite the
140 nonlinear dynamics at play, the simulated shift in the CX model closely resembled the
141 response of the ants to the sun manipulation, adding credibility to the model and helping us
142 grasp the mechanisms at play (Fig. 4).

143

144 ***General discussion***

145 We showed that during view-based navigation, ants recognise views when oriented left and
146 right from their goal to trigger left and right turns. Facing in the correct route direction does
147 not trigger a 'go forward' command, but marks some kind of labile equilibrium point in the
148 system. Also, we show that the recognition of left or right familiar views does not drive the

149 motor decision directly but is perfectly suited to inform the CX, which in turn maintains the
150 desired heading using its own compass information. The advantage of this design is clear
151 considering that the recognition of learnt visual terrestrial cues is sensitive to variables such
152 as body orientation^{31,32} or partial visual obstructions that must happen continuously when
153 navigating through grassy or leafy environments, making the visual familiarity signal
154 mediated by the MBs inherently noisy. In contrast, the CX provides a stable and sustained
155 heading representation by integrating self-motion¹¹ with multiple wide-field celestial¹⁰ and
156 terrestrial cues^{9,33}. The CX is thus well suited to act as a heading buffer from the noisy MBs
157 signal, resulting in smooth and stable guidance control. In addition, the compass
158 representation in the CX enables to steer the direction of travel independently of the actual
159 body orientation¹². Our results thus explain how ants visually recognise a view using the
160 MBs and subsequently follow such direction backwards using the CX³¹ or how ants can
161 estimate the actual angular error between the current and goal directions before initiating
162 their turn³⁴. Also, in addition to route following, such a lateralised design can produce
163 remarkably robust homing in complex environments (Wystrach et al., 2020 in prep).

164 Finally, the proposed circuit offers an interesting take on the evolution of navigation.
165 Segregating ‘turn left’ and ‘turn right’ signals between hemispheres evokes the widespread
166 tropotaxis, where orientation along a gradient is achieved by directly comparing the signals
167 intensities between physically distinct left and right sensors (e.g., antennae or eyes) in
168 bilateral animals^{35–41}. Comparing signals between hemispheres could thus be an ancestral
169 strategy in arthropods; and ancestral brain structures such as the CX accommodates well
170 such a bilateral design and may be constrained to receive such lateralised input to function
171 properly. The evolution of visual route-following in hymenoptera is a relatively recent
172 adaptation, and it cannot be achieved by directly comparing left and right visual inputs –
173 which is probably why each eye can afford to project to both hemispheres’ MBs^{42,43}.
174 Categorising learnt views as indicators of whether the goal is to the left or to the right, and
175 subsequently segregating this information in the left and right hemispheres may thus be an
176 evolutionary adaptation to fit the ancestrally needed bilateral inputs to the CX (Fig. 1).

177 How left and right visual memories are acquired and learnt when naive insects explore the
178 world for the first time remains to be seen. During their learning flights, wasps regularly
179 alternate between moments facing 45° to the left and 45° to the right of their goal, strongly

180 supporting our claim that insect form such left and right memories⁴⁴. During their
181 meandering learning walks, ants tend to reverse turning direction when facing the nest or
182 anti-nest direction^{21,23,45}, however, they do expose their gaze in all directions, providing
183 ample opportunities to form a rich set of left and right visual memories⁴⁵. Our model shows
184 that the angle at which views are learnt does not need to be precisely controlled (Fig. 1c,d).
185 Views facing the nest may as well be included during learning and categorised as left, right or
186 both, explaining why most ants facing their goal usually choose to turn in one particular
187 direction while others turned less strongly. During learning, the first source of information
188 about whether the current body orientation is left or right from the goal probably results
189 from path integration. Interestingly, lateralised dopaminergic feedback from the Lateral
190 Accessory Lobes (LAL, a pre-motor area) to the MBs could represent an ideal candidate to
191 orchestrate such a categorisation of left/right memories (Wystrach et al., 2020 in prep).
192 Revisiting current questions in insect and robot navigation such as early exploration, route
193 following and homing^{20,46-49}, the integration of aversive memories^{8,24,50}, path integration
194 and views⁵¹⁻⁵⁴ or other sensory modalities⁵⁵⁻⁵⁸ as well as seeking for underlying neural
195 correlates⁵⁻⁷ – with such a lateralised design as a framework promises an interesting
196 research agenda.

197

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202 earlier versions of the manuscript.

203 **Authors contributions**

204 Research design: AW. Data collection: AW, SS, FLM, LC. Trackball system design: FLM. Data
205 analysis: AW, SS, FLM. Modelling: AW. Manuscript writing: AW.

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208

209 **Method**

210 *The trackball setup:*

211 For both experiments (fig 2 and 3) we used the air-suspended trackball setup as described in
212 Dahmen et al., 2017²⁹; and chose the configuration where the ants are fixed in a given
213 direction and cannot physically rotate (if the ant tries to turn, the ball counter-rotates under
214 its legs). To fix ants on the ball, we used a micro-magnet and metallic paint applied directly
215 on the ant's thorax. The trackball air pump, battery and computer were connected to the
216 trackball through 10 m long cables and hidden in a remote part of the panorama. The
217 trackball movements were recorded using custom software in C++, data was analysed with
218 Matlab and can be provided upon request.

219

220 *Routes setups and ant training in *Cataglyphis velox*:*

221 For all experiments (fig. 2 and 3 and 4), *Cataglyphis velox* ants were constrained to forage
222 within a route using dug wood planks that prevented them to escape, while leaving the
223 surrounding panoramic view of the scenery intact (as described in Wystrach et al., 2012⁵⁹).
224 Cookie crumbs were provided ad libitum in the feeder positions for at least two days before
225 any tests. Some barriers dug into the ground created baffles, enabling us to control whether
226 ants were experienced with the route. Ants were considered trained when able to home
227 along the route without bumping into any such obstacle. These ants were captured just
228 before they entered their nest to ensure that they could not rely on path integration (so-
229 called ZV ants), marked with a metallic paint on the thorax and a colour code for individual
230 identification, and subjected to tests (see next sections).

231

232 *Routes setups and ant training in *Myrmecia croslandi*:*

233 For the experiment with *Myrmecia croslandi* ants (fig. 2), we used each individual's natural
234 route, for which these long-lived ants have extensive experience⁶⁰. Individuals were
235 captured on their foraging trees, marked with both metallic paint and a colour code for
236 individual identification, given a sucrose solution or a prey and released where they had
237 been captured (on their foraging tree). Upon release, most of these ants immediately started

238 to return home. We followed them while marking their route using flag pins every 50 cm (so
239 that their exact route was known). We captured the ants just before they entered their nests
240 and subjected them to the test on the trackball (see next section).

241

242 *Experimental protocol for the left/right trackball experiment (figure 2):*

243

244 1- An experienced ant was captured just before entering its nest, and marked with a drop of
245 metallic paint on the thorax.

246 2- A large opaque ring (30 cm diameter, 30 cm high) was set around the trackball setup.

247 3- The ant was fixed on the trackball within the opaque ring, which prevented her to see the
248 surroundings. Only a portion of sky above was accessible to the ant.

249 4- The trackball system (together with the opaque ring and the fixed ant within) was moved
250 to the desired position and rotated so that the ant was facing the desired direction.

251 5- One experimenter started recording the trackball movements (from the remote
252 computer), when another lifted the ring (so the ant could see the scenery) before leaving the
253 scene, letting the ant behave for at least 15 seconds post ring lifting.

254 6- The experimenter came back, replaced the ring around the trackball system, and rotated
255 the trackball system (following a pre-established pseudo random sequence) for the ant to
256 face in a novel direction.

257 7- We repeated steps 5 and 6 until the 8 possible orientations were achieved (the sequence
258 of orientations were chosen in a pseudo-random order so as to counter-balance orientation
259 and direction of rotation).

260 The data shown in fig. 2 for each orientation is averaged across 12 sec of recording (from 3
261 sec to 15 sec assuming ring lifting is at 0 sec). We decided to let 3 sec after ring lifting, as the
262 movements of the experimenter before he leaves the scenery might disturb the ants).

263 In all experiments, ants were tested only once.

264

265 *Experimental protocol for the mirror trackball experiments (figure 3):*

266

267 1- An experienced ant was captured just before entering its nest, and marked with a drop of
268 metallic paint on the thorax.

269 2- A large opaque ring (30 cm diameter, 30 cm high) was set around the trackball setup.
270 3- The ant was fixed on the trackball within the opaque ring, which prevented her to see the
271 surroundings. Only a portion of sky above was accessible to the ant.
272 4- The trackball system (together with the opaque ring and the fixed ant within) was moved
273 to the desired position and rotated so that the ant was facing the desired direction.
274 5- One experimenter started recording the trackball movements, when another lifted the
275 ring (so the ant could see the scenery) before leaving the scene, letting the ant behave for at
276 least 10 seconds post ring lifting.
277 5- Two experimenters simultaneously hid the real sun and projected the reflected sun using
278 a mirror, so that the sun appeared in the opposite position of the sky to the ant for at least 8
279 seconds.
280 Ants were tested only once, in one of the conditions.

281

282 *Experimental design and protocol for the mirror experiment with ants on the floor (figure 4):*

283

284 *Cataglyphis velox* ants were trained to a 10 meters-long route for at least two consecutive
285 days. A 240 × 120 cm thin wood board was placed on the floor in the middle of the route,
286 ensuring that the navigating ants walked smoothly without encountering small clutter over
287 this portion of the route. Homing ants were captured just before entering their nest and
288 released at the feeder as ZV ants. Upon release, these ZV ants typically resume their route
289 homing behaviour; at mid-parkour (halfway along the board section) the real sun was hidden
290 by one experimenter and reflected by another, using a mirror, for the sun to appear to the
291 ant 135° away from its original position in the sky. To ensure that each individual was tested
292 only once, tested ants were marked with a drop of paint after the procedure.

293 The ZV ants walking on the board were recorded using a Panasonic Lumix DMC-FZ200
294 camera on a tripod, and their paths were digitised frame by frame at 10 fps using image J.
295 We used four marks on the board to correct for the distortion due to the tilted perspective
296 of the camera's visual field. Analysis of the paths were achieved with Matlab.

297

298

299 *The CX neural model.*

300 The CX model circuitry and input signals are described in Extended data figure 2 (a-d), and
301 the different parameters used to obtain the output (motor command) are described in
302 Extended data figure 1. All the modelling has been achieved with Matlab, and can be
303 provided upon request.

304

305 **References**

- 306 1. Collett, M., Chittka, L. & Collett, T. S. Spatial memory in insect navigation. *Current biology : CB* **23**,
307 R789–R800 (2013).
- 308 2. Collett, T. S. & Collett, M. Path integration in insects. *Current Opinion in Neurobiology* **10**, 757–
309 762 (2000).
- 310 3. Wystrach, A., Schwarz, S., Schultheiss, P., Baniel, A. & Cheng, K. Multiple sources of celestial
311 compass information in the central Australian desert ant *Melophorus bagoti*. *Journal of*
312 *Comparative Physiology A* 1–11 (2014).
- 313 4. Ardin, P., Peng, F., Mangan, M., Lagogiannis, K. & Webb, B. Using an Insect Mushroom Body
314 Circuit to Encode Route Memory in Complex Natural Environments. *PLOS Computational Biology*
315 **12**, e1004683 (2016).
- 316 5. Buehlmann, C. *et al.* Mushroom Bodies Are Required for Learned Visual Navigation, but Not for
317 Innate Visual Behavior, in Ants. *Current Biology* (2020) doi:10.1016/j.cub.2020.07.013.
- 318 6. Kamhi, J. F., Barron, A. B. & Narendra, A. Vertical Lobes of the Mushroom Bodies Are Essential
319 for View-Based Navigation in Australian Myrmecia Ants. *Current Biology* (2020)
320 doi:10.1016/j.cub.2020.06.030.
- 321 7. Webb, B. & Wystrach, A. Neural mechanisms of insect navigation. *Current Opinion in Insect*
322 *Science* **15**, 27–39 (2016).
- 323 8. Wystrach, A., Buehlmann, C., Schwarz, S., Cheng, K. & Graham, P. Rapid Aversive and Memory
324 Trace Learning during Route Navigation in Desert Ants. *Current Biology* **30**, 1927–1933.e2 (2020).
- 325 9. Kim, S. S., Hermundstad, A. M., Romani, S., Abbott, L. F. & Jayaraman, V. Generation of stable
326 heading representations in diverse visual scenes. *Nature* **576**, 126–131 (2019).
- 327 10. Pfeiffer, K. & Homberg, U. Organization and Functional Roles of the Central Complex in the Insect
328 Brain. *Annual Review of Entomology* **59**, null (2014).
- 329 11. Seelig, J. D. & Jayaraman, V. Neural dynamics for landmark orientation and angular path
330 integration. *Nature* **521**, 186–191 (2015).

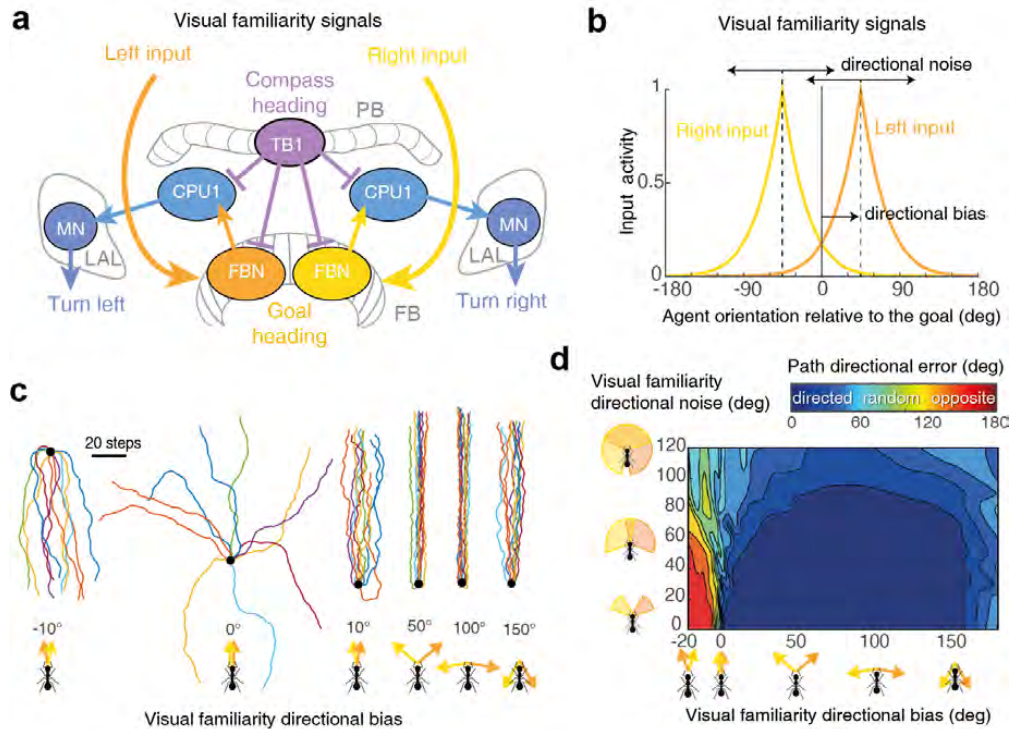
- 331 12. Stone, T. *et al.* An Anatomically Constrained Model for Path Integration in the Bee Brain. *Current*
332 *Biology* **27**, 3069-3085.e11 (2017).
- 333 13. Collett, M. & Collett, T. S. How does the insect central complex use mushroom body output for
334 steering? *Current Biology* **28**, R733–R734 (2018).
- 335 14. Honkanen, A., Adden, A., Freitas, J. da S. & Heinze, S. The insect central complex and the neural
336 basis of navigational strategies. *Journal of Experimental Biology* **222**, jeb188854 (2019).
- 337 15. Franconville, R., Beron, C. & Jayaraman, V. Building a functional connectome of the Drosophila
338 central complex. *eLife* **7**, e37017 (2018).
- 339 16. Le Moël, F., Stone, T., Lihoreau, M., Wystrach, A. & Webb, B. The Central Complex as a Potential
340 Substrate for Vector Based Navigation. *Front. Psychol.* **10**, (2019).
- 341 17. Pisokas, I., Heinze, S. & Webb, B. The head direction circuit of two insect species. *eLife* **9**, e53985
342 (2020).
- 343 18. Heinze, S. & Homberg, U. Maplike representation of celestial E-vector orientations in the brain of
344 an insect. *Science* **315**, 995–997 (2007).
- 345 19. Green, J., Vijayan, V., Pires, P. M., Adachi, A. & Maimon, G. A neural heading estimate is
346 compared with an internal goal to guide oriented navigation. *Nature neuroscience* **22**, 1460–
347 1468 (2019).
- 348 20. Fleischmann, P. N., Rössler, W. & Wehner, R. Early foraging life: spatial and temporal aspects of
349 landmark learning in the ant *Cataglyphis noda*. *Journal of Comparative Physiology A* **204**, 579–
350 592 (2018).
- 351 21. Müller, M. & Wehner, R. Path Integration Provides a Scaffold for Landmark Learning in Desert
352 Ants. *Current Biology* **20**, 1368–1371 (2010).
- 353 22. Wystrach, A., Mangan, M., Philippides, A. & Graham, P. Snapshots in ants? New interpretations
354 of paradigmatic experiments. *The Journal of Experimental Biology* **216**, 1766–1770 (2013).
- 355 23. Jayatilaka, P., Murray, T., Narendra, A. & Zeil, J. The choreography of learning walks in the
356 Australian jack jumper ant *Myrmecia croslandi*. *Journal of Experimental Biology* **221**, jeb185306
357 (2018).
- 358 24. Möel, F. L. & Wystrach, A. Opponent processes in visual memories: A model of attraction and
359 repulsion in navigating insects' mushroom bodies. *PLOS Computational Biology* **16**, e1007631
360 (2020).
- 361 25. Murray, T. *et al.* The role of attractive and repellent scene memories in ant homing (*Myrmecia*
362 *croslandi*). *Journal of Experimental Biology* (2019) doi:10.1242/jeb.210021.
- 363 26. Baddeley, B., Graham, P., Husbands, P. & Philippides, A. A model of ant route navigation driven
364 by scene familiarity. *PLoS Comput Biol* **8**, e1002336 (2012).

- 365 27. Wystrach, A., Cheng, K., Sosa, S. & Beugnon, G. Geometry, features, and panoramic views: Ants
366 in rectangular arenas. *Journal of Experimental Psychology: Animal Behavior Processes* **37**, 420–
367 435 (2011).
- 368 28. Zeil, J. Visual homing: an insect perspective. *Current Opinion in Neurobiology* **22**, 285–293 (2012).
- 369 29. Dahmen, H., Wahl, V. L., Pfeffer, S. E., Mallot, H. A. & Wittlinger, M. Naturalistic path integration
370 of *Cataglyphis* desert ants on an air-cushioned lightweight spherical treadmill. *Journal of*
371 *Experimental Biology* **220**, 634–644 (2017).
- 372 30. Wehner, R., Michel, B. & Antonsen, P. Visual navigation in insects: Coupling of egocentric and
373 geocentric information. *Journal of Experimental Biology* **199**, 129–140 (1996).
- 374 31. Schwarz, S., Mangan, M., Zeil, J., Webb, B. & Wystrach, A. How Ants Use Vision When Homing
375 Backward. *Current Biology* **27**, 401–407 (2017).
- 376 32. Zeil, J., Hofmann, M. I. & Chahl, J. S. Catchment areas of panoramic snapshots in outdoor scenes.
377 *Journal of the Optical Society of America a-Optics Image Science and Vision* **20**, 450–469 (2003).
- 378 33. Fisher, Y. E., Lu, J., D'Alessandro, I. & Wilson, R. I. Sensorimotor experience remaps visual input
379 to a heading-direction network. *Nature* **576**, 121–125 (2019).
- 380 34. Lent, D. D., Graham, P. & Collett, T. S. Image-matching during ant navigation occurs through
381 saccade-like body turns controlled by learned visual features. *Proceedings of the National*
382 *Academy of Sciences of the United States of America* **107**, 16348–16353 (2010).
- 383 35. Borst, A. & Heisenberg, M. Osmotropotaxis in *Drosophila melanogaster*. *Journal of comparative*
384 *physiology* **147**, 479–484 (1982).
- 385 36. Cain, W. S. Differential sensitivity for smell: "noise" at the nose. *Science* **195**, 796–798 (1977).
- 386 37. Duistermars, B. J., Chow, D. M. & Frye, M. A. Flies require bilateral sensory input to track odor
387 gradients in flight. *Current Biology* **19**, 1301–1307 (2009).
- 388 38. Jékely, G. *et al.* Mechanism of phototaxis in marine zooplankton. *Nature* **456**, 395–399 (2008).
- 389 39. Martin, H. Osmotropotaxis in the honey-bee. *Nature* **208**, 59–63 (1965).
- 390 40. Matsuo, Y., Uozumi, N. & Matsuo, R. Photo-tropotaxis based on projection through the cerebral
391 commissure in the terrestrial slug *Limax*. *Journal of Comparative Physiology A* **200**, 1023–1032
392 (2014).
- 393 41. Porter, J. *et al.* Mechanisms of scent-tracking in humans. *Nature neuroscience* **10**, 27–29 (2007).
- 394 42. Habenstein, J., Amini, E., Grübel, K., el Jundi, B. & Rössler, W. The brain of *Cataglyphis* ants:
395 neuronal organization and visual projections. *Journal of Comparative Neurology* (2020).
- 396 43. Rössler, W. Neuroplasticity in desert ants (Hymenoptera: Formicidae)—importance for the
397 ontogeny of navigation. *Myrmecological News* **29**, (2019).
- 398 44. Stürzl, W., Zeil, J., Boeddeker, N. & Hemmi, J. M. How Wasps Acquire and Use Views for Homing.
399 *Current Biology* **26**, 470–482 (2016).

- 400 45. Zeil, J. & Fleischmann, P. N. The learning walks of ants (Hymenoptera: Formicidae). (2019).
- 401 46. Denuelle, A. & Srinivasan, M. V. Bio-inspired visual guidance: From insect homing to UAS
402 navigation. in *2015 IEEE International Conference on Robotics and Biomimetics (ROBIO)* 326–332
403 (IEEE, 2015).
- 404 47. Kodzhabashev, A. & Mangan, M. Route Following Without Scanning. in *Biomimetic and Biohybrid*
405 *Systems* 199–210 (Springer, 2015).
- 406 48. Möller, R. Insect visual homing strategies in a robot with analog processing. *Biological*
407 *Cybernetics* **83**, 231–243 (2000).
- 408 49. Philippides, A., de Ibarra, N. H., Riabinina, O. & Collett, T. S. Bumblebee calligraphy: the design
409 and control of flight motifs in the learning and return flights of *Bombus terrestris*. *The Journal of*
410 *Experimental Biology* **216**, 1093–1104 (2013).
- 411 50. Schwarz, S., Clement, L., Gkaniyas, E. & Wystrach, A. *How do backward walking ants (Cataglyphis*
412 *velox) cope with navigational uncertainty?*
413 <http://biorxiv.org/lookup/doi/10.1101/2019.12.16.877704> (2019)
414 doi:10.1101/2019.12.16.877704.
- 415 51. Freas, C. A. & Cheng, K. Limits of vector calibration in the Australian desert ant, *Melophorus*
416 *bagoti*. *Insect. Soc.* **65**, 141–152 (2018).
- 417 52. Hoinville, T. & Wehner, R. Optimal multiguideance integration in insect navigation. *Proceedings of*
418 *the National Academy of Sciences* **115**, 2824–2829 (2018).
- 419 53. Wehner, R., Hoinville, T., Cruse, H. & Cheng, K. Steering intermediate courses: desert ants
420 combine information from various navigational routines. *J Comp Physiol A* **202**, 459–472 (2016).
- 421 54. Wystrach, A., Mangan, M. & Webb, B. Optimal cue integration in ants. *Proceedings of the Royal*
422 *Society of London B: Biological Sciences* **282**, (2015).
- 423 55. Buehlmann, C., Mangan, M. & Graham, P. Multimodal interactions in insect navigation. *Animal*
424 *Cognition* 1–13 (2020).
- 425 56. Buehlmann, C., Graham, P., Hansson, B. S. & Knaden, M. Desert ants locate food by combining
426 high sensitivity to food odors with extensive crosswind runs. *Current Biology* **24**, 960–964 (2014).
- 427 57. Knaden, M. & Graham, P. The sensory ecology of ant navigation: from natural environments to
428 neural mechanisms. *Annual review of entomology* **61**, 63–76 (2016).
- 429 58. Wystrach, A. & Schwarz, S. Ants use a predictive mechanism to compensate for passive
430 displacements by wind. *Current biology : CB* **23**, R1083–R1085 (2013).
- 431 59. Wystrach, A., Beugnon, G. & Cheng, K. Ants might use different view-matching strategies on and
432 off the route. *The Journal of Experimental Biology* **215**, 44–55 (2012).

- 433 60. Narendra, A., Gourmaud, S. & Zeil, J. Mapping the navigational knowledge of individually
434 foraging ants, *Myrmecia croslandi*. *Proceedings of the Royal Society B: Biological Sciences* **280**,
435 (2013).
- 436 61. Green, J. & Maimon, G. Building a heading signal from anatomically defined neuron types in the
437 *Drosophila* central complex. *Current Opinion in Neurobiology* **52**, 156–164 (2018).
438

439 **Figure 1**



440

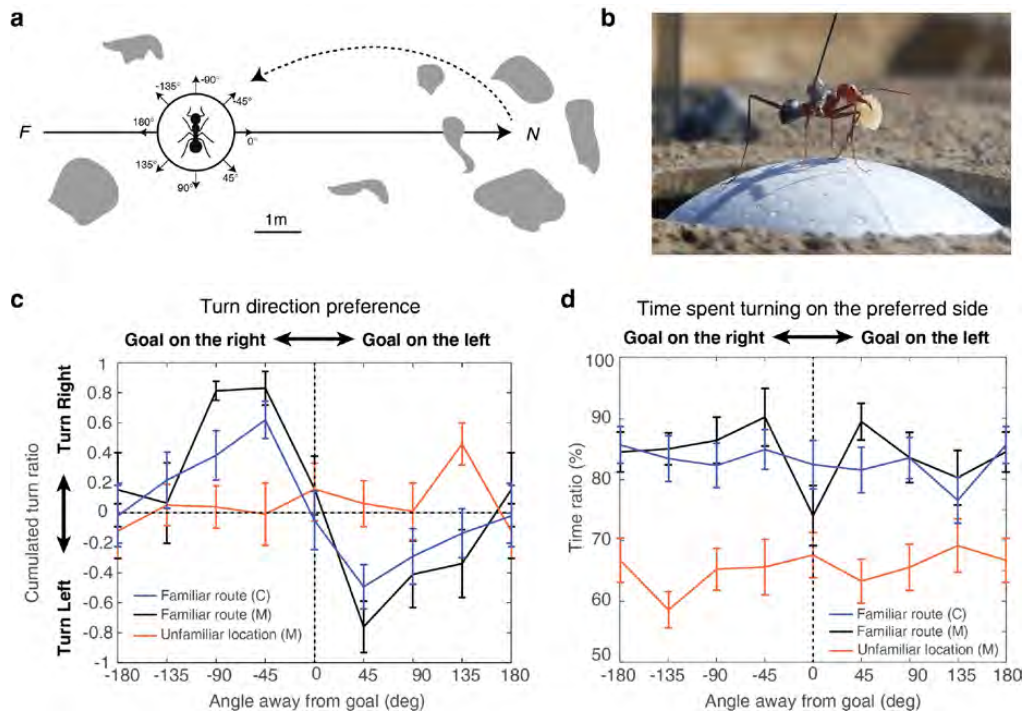
441 **Figure 1. Bilaterally decorrelated input to Central Complex produces stable route heading.**

442 **a.** The central complex (CX) sits at the centre of the brain but is wired to both hemispheres.
 443 It receives bilateral inputs in the Fan-shaped Body (FB), where sustained activity of the FB
 444 neurons (FBN) forms two representations of the goal heading. CPU1 neurons compare such
 445 ‘goal heading’ representations to the ‘compass-based current heading’ representation of the
 446 Protocerebral Bridge (PB) neurons (TB1) and outputs bilateral signals to the left and right
 447 Lateral Accessory Lobes (LALs), where they modulate motor neurons (MN) descending to the
 448 thorax to control left and right turns, respectively (see **extended figure 2, d, g** for details of
 449 the circuitry). **b.** Simulated inputs to the FBN neurons. We assumed that the input signals to
 450 the FBN are body-orientation-dependant (as expected if resulting from visual familiarity of
 451 the scene²⁸ such as outputted by the MBs⁴. ‘directional bias’ indicates the direction relative
 452 to the goal direction (0°) at which the left visual familiarity signals is highest in average (+45°
 453 in this example). Right signal responds symmetrically for the other direction (-directional
 454 bias). ‘Directional noise’ in the visual familiarity was implemented by shifting the input curve
 455 relative to its mean (i.e. the ‘directional bias’) at each time step by a random value

456 (normal distribution with standard deviation given by 'directional noise'). **c.** Paths resulting
457 given different directional biases. **d.** Path directional error (absolute angular error between
458 start-to-arrival beeline, and start-to-goal direction) after 200 steps, as a function of the visual
459 familiarity 'directional bias' (x axis) and 'directional noise' (y axis). **c, d.** Straight route
460 headings robustly emerge as long as left and right inputs send a signal when the body is
461 oriented right and left from the goal, respectively (i.e., directional bias $> 0^\circ$) but not if both
462 inputs send a signal when facing the goal (i.e., directional bias = 0°). Orientation towards the
463 opposite direction emerges if left and right inputs signal inversely, that is, when the body is
464 oriented right and left from the goal respectively (i.e., directional bias $< 0^\circ$). Robustness to
465 visual familiarity directional noise indicate that the direction in which views are learnt does
466 not need to be precisely controlled. See further analysis in Extended Data Fig. 1.

467

468 **Figure 2.**

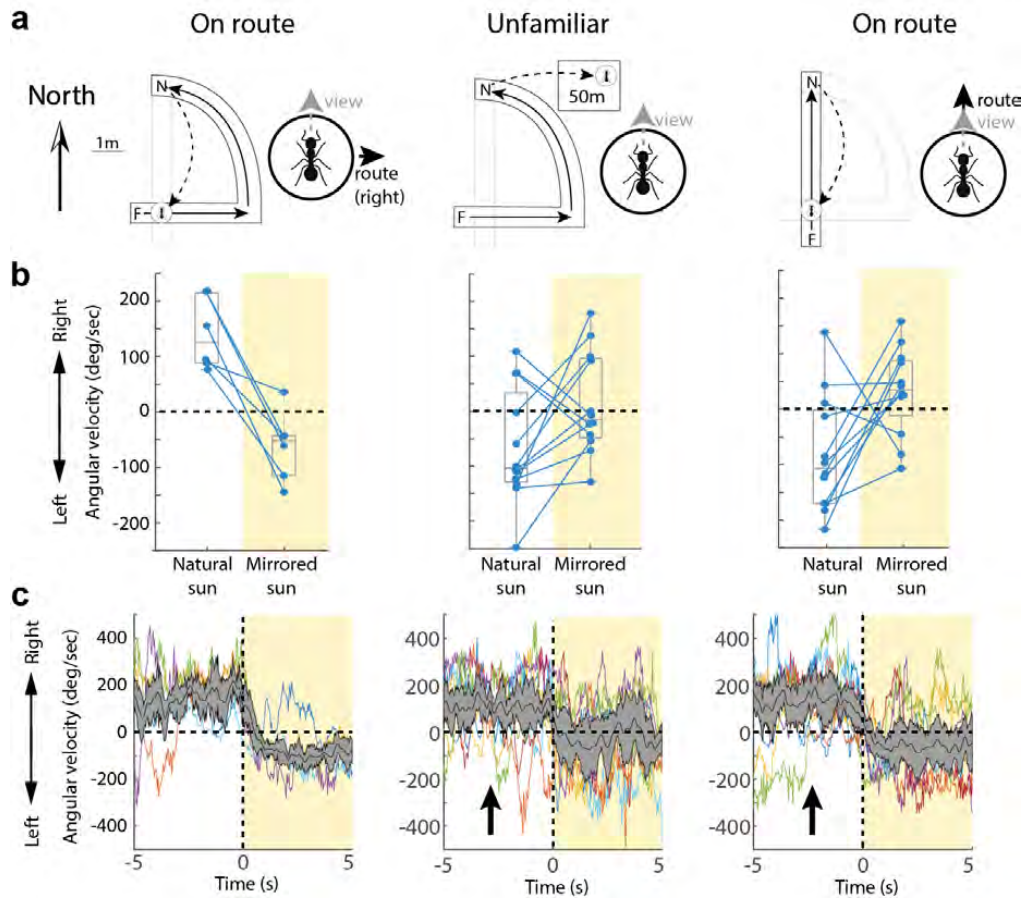


469

470 **Figure 2. Ants visually recognise whether the goal direction is left or right.** **a.** Homing ants
 471 were captured at the end of their familiar route and fixed on the trackball **(b)** in 8 different
 472 compass orientations. The route was rich in visual terrestrial cues (grey blobs). *F*: feeder, *N*:
 473 nest. **b.** An individual *Cataglyphis velox* mounted on the trackball setup, holding its precious
 474 cookie crumb. **c.** Turn ratio (degrees (*right - left*) / (*right + left*); mean ± se across individuals)
 475 for the eight compass directions, on the familiar route or in the unfamiliar location (same
 476 compass directions but unfamiliar surroundings) across 12 seconds of recording. **d.**
 477 Proportion of time spent turning on the preferred side of each individual (mean ± se across
 478 individuals). *C*: *Cataglyphis velox* (*n*=17), *M*: *Myrmecia crosslandi* (*n*=11).

479

480 **Figure 3**



481

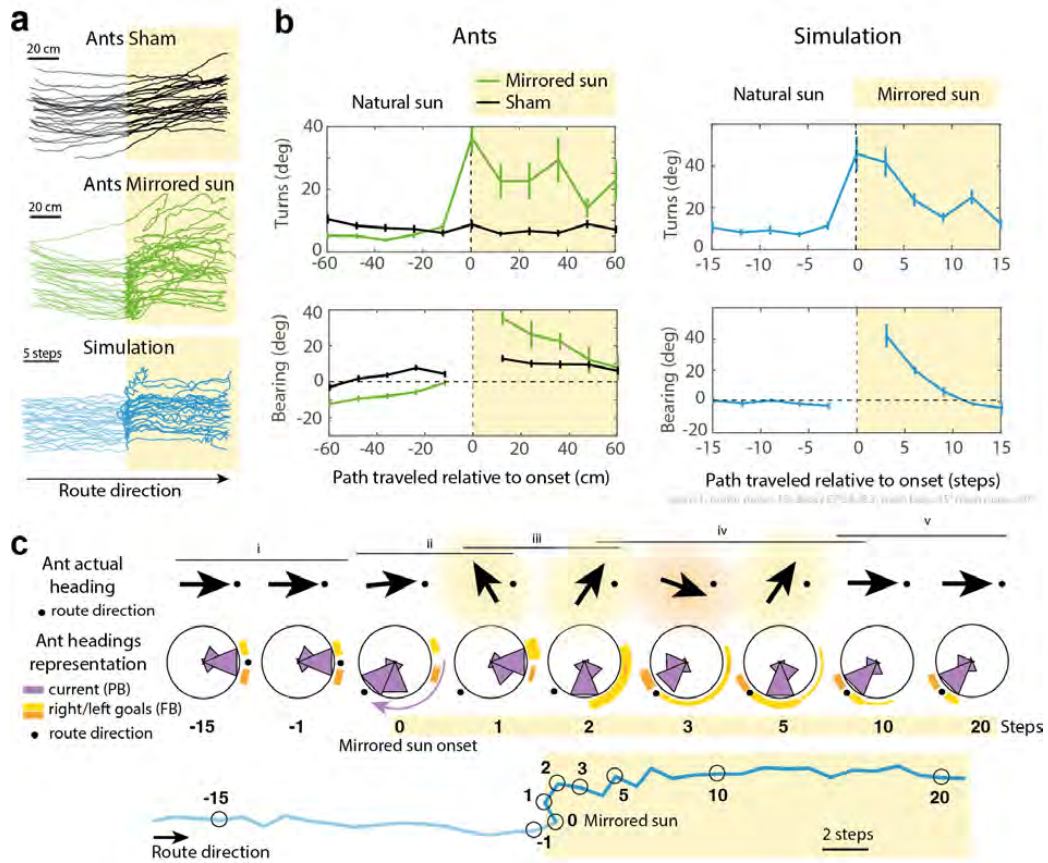
482 **Figure 3. Rotation of celestial cues shift turning direction based on familiar terrestrial cues.**

483 **a.** Schemes of the training and test condition. Homing ants were captured at the end of their
 484 familiar route (black arrows: familiar route, F: feeder, N: nest) and fixed on the trackball with
 485 their body always facing north, either on their route with the route direction 90° to the right
 486 (left panel); or within unfamiliar surroundings (middle panel); or ants were trained along a
 487 route oriented 90° to the previous one and released on their familiar route in the same
 488 location and orientation, which this time is facing their route direction. **b.** Box plots indicate
 489 average angular velocity (positive = right turn) each ant (dots) 5s before (white) and 5s after
 490 (yellow) the apparent sun's position is mirrored by 180°. Wilcoxon test for: 'turn towards
 491 the right with natural sun' (left panel: n=6, p=0.0156; middle panel: n=12 p=0.9788; right
 492 panel: n=12 p=0.9866), 'mirror effect: turn direction reversal' (left panel: n=6, p=0.0156,
 493 power=0.9994; middle panel: n=12 p=0.3955; right panel: n=12 p=0.0320). **c.** Turning

494 velocities (individuals in colour; median \pm iqr of the distribution in grey) across time, before
495 and after the sun manipulation (t_0). Arrows in the middle and left panels: the velocities of
496 some individuals have been inverted so that all individuals' mean turn directions before the
497 manipulation are positive.

498

499 **Figure 4**



500

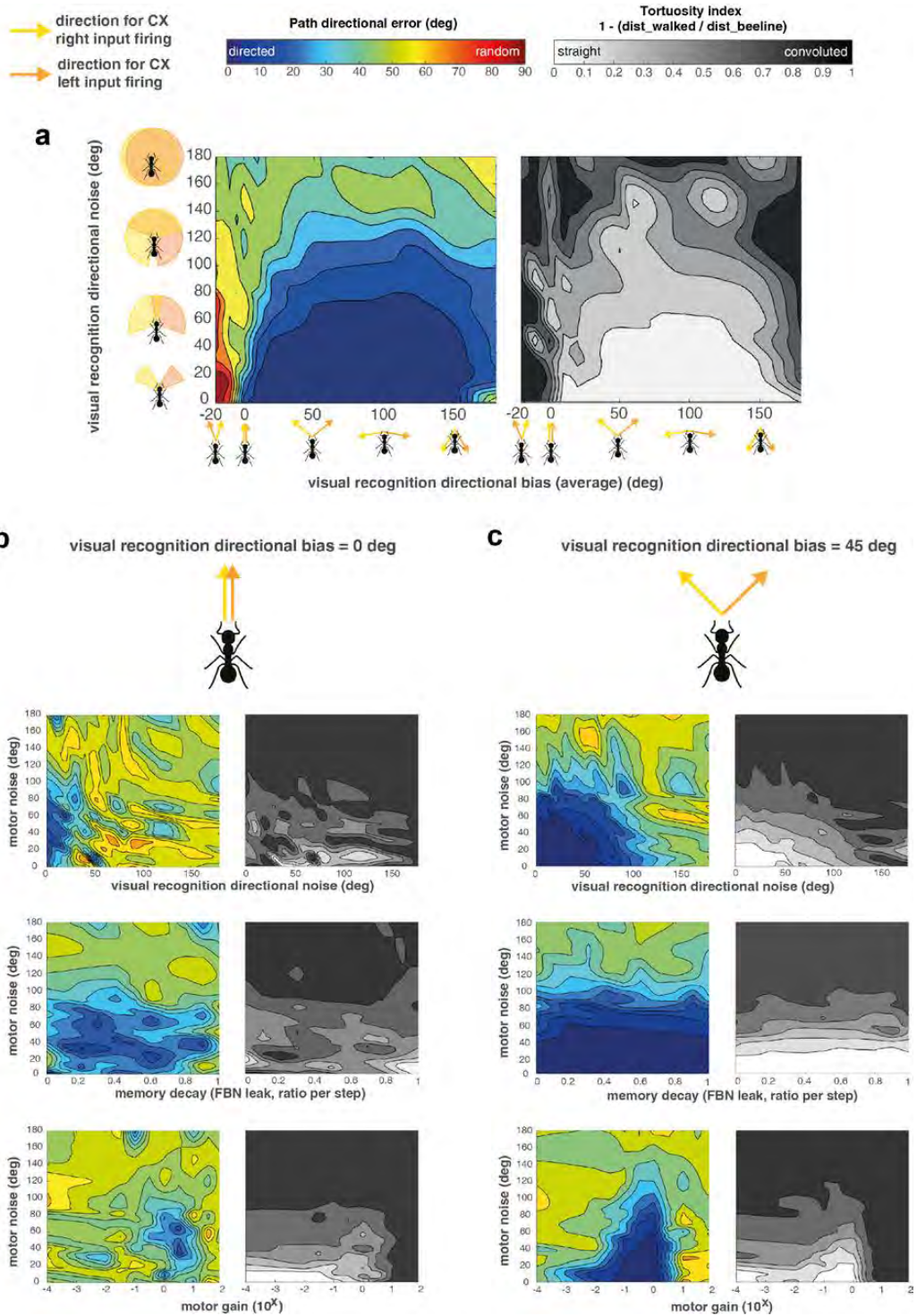
501 **Figure 4. Rotation of celestial cues affect ants route following as predicted.** Paths (a) and
 502 quantification of bearing and turns (b) of real (black and green) and simulated (blue) zero-
 503 vector ants (i.e., deprived of path integration information) recapitulating a familiar straight
 504 route while entering an area where we manipulated celestial compass cues (yellow). For the
 505 ‘Mirrored sun’ condition (green) the real sun was hidden from the ants and mirrored so as to
 506 appear rotated by 135° counter clockwise in the sky. For the ‘sham’ condition (black), the
 507 experimenters were standing in the same place and the real sun was also hidden, but only a
 508 small piece of the sky (close to, but not including the sun) was mirrored for the ants.
 509 Simulated ants (blue) result from the model presented in fig. 1. Sun rotation was modelled
 510 as a 135° shift in the current heading representation (3-cell shift of the bump of activity in
 511 the Protocerebral Bridge). Paths of both real and simulated ants were discretised (segments
 512 of 12 cm for real ants, and of 3 steps for the simulations), before and after the sun rotation
 513 onset point. Turns correspond to the absolute angle between two successive segments,

514 bearing indicates the direction of segments relative to the route (0°). Turns at '0' on the x-
515 axes correspond to the angle between the segment preceding and following the shift of the
516 celestial compass. **c.** The effect observed in the simulations is quantitatively dependant on
517 the model's parameters (here gain=1; motor noise=10; decay FBN=0.2; visual familiarity
518 directional bias \pm noise=45° \pm 10° see Extended Data Fig. 1 for a description of parameters),
519 but its key signature can be explained qualitatively. (i) Under normal situation the current
520 heading is maintained between the right and left goal heading representation in the Fan-
521 shaped Body (FB) (yellow and orange marks) and updated by right and left visual familiarity
522 signals. (ii) The sun rotation creates a sudden shift of the current heading representation in
523 the Protocerebral Bridge (PB) (purple curved arrow), although the agent is still physically
524 facing the actual route direction (black dot). This leads the agent to display a sudden left
525 turn to re-align its shifted heading representation with the FB goal heading that is held in
526 short term memory. (iii) This novel direction of travel is visually recognised as being 'left of
527 the goal', causing a strong lateralised signal in the right FB's goal heading representation
528 (yellow). This biased activity triggers right turns, exposing the agent to new headings
529 recognised as 'right of the goal', and thus more signal sent to the right FB (yellow arcs),
530 favouring further right turns. (iv) Turning right eventually leads the agent to overshoot the
531 actual goal direction, recognise view as 'right from the goal' and thus signalling in the left FB
532 (orange). These signals are, at first, superimposed with the previous desired heading
533 representation, resulting in a period of conflicting guidance information causing meandering.
534 (v) The agent progressively updates its novel goal heading representation as the trace of the
535 previous desired heading fades out and the new one strengthens due to the incoming signals
536 from visual familiarity. In sum, motor decision results from complex dynamics between two
537 main factors: 1- how strong are the left and right visual familiarity signals updating the goal
538 heading representations (orange and yellow glow around the 'Ant actual heading' arrows),
539 which depend on whether the agent is oriented left or right from its goal; and 2- how well
540 the current heading representation (PB) matches the goal heading representation (more
541 detail in Extended Data Fig. 2).

542

543

544 **Extended data figure 1.**



545

546 **Extended data figure 1. Parameter exploration of the Central Complex model (see fig 3). a.**

547 This shows a parameter exploration for the CX model presented in **Fig. 1** (see **extended fig. 2**
548 for details of the circuitry). - Path directional error (absolute angular error between start-to-
549 arrival and start-to-goal directions) and path tortuosity (index = $1 -$
550 $(\text{beeline_distance}/\text{distance_walked})$) after 200 steps are shown according to various
551 parameter ranges. For each point on the map, all the other parameters are chosen to
552 maximise for lowest path directionality error.

553 **a.** Same as **Fig. 1d**, except that for each point of the map, the other parameters are chosen
554 to maximise for lowest path directionality error instead of being fixed at an average range.
555 Note that in **Fig. 1d**, visual familiarity direction bias < 0 typically results in routes leading to
556 the opposite direction (i.e., path directional error close to 180° , see **Fig. 1**). Here, maximising
557 for lowest path directional error did not result in goal-oriented path, but selected
558 parameters yielding very high tortuosity, thus indicated that no parameter regime can yield
559 straight, directed route when visual familiarity bias is < 0 . Note that straight, goal-oriented
560 paths emerge as long as the visual familiarity direction bias is > 0 , that is, if the left
561 hemisphere inputs correlate with moments when the nest is on the left, and vice versa.

562 **b.** Visual familiarity directional bias is fixed at a value of 0° , meaning that both CX inputs
563 respond maximally when the agent is facing the goal direction. Note that in this condition,
564 regions of low path directional errors (blue) and region of low path tortuosity (white) do not
565 overlap. This means that one cannot obtain straight, goal-directed paths if left and right CX
566 inputs respond when the nest is located in front.

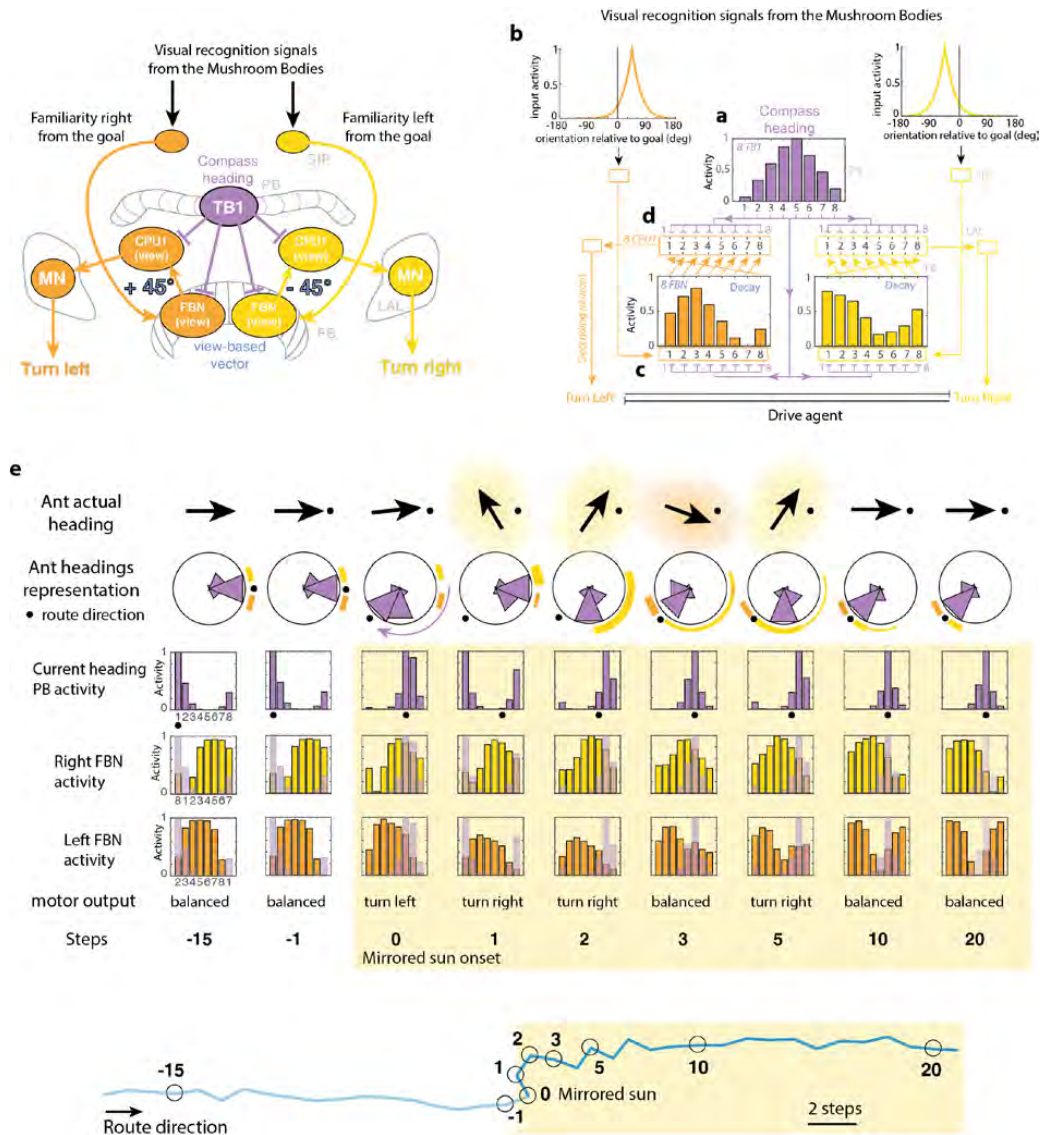
567 **c.** Visual familiarity directional bias is fixed at a value of $+45^\circ$, meaning that left and right CX
568 inputs respond maximally when the agent is oriented 45° to the right or left from the goal
569 direction, respectively. Note that regions with low path directional errors (blue) and regions
570 of low path tortuosity (white) overlap well, showing a very large range of parameters for
571 which we can obtain straight, goal-directed paths. We found the robustness to parameters
572 remarkable: the model copes with motor noise up to 80° , visual familiarity direction noise up
573 to 90° , is insensitive to its vector-memory decay and operates across several orders of
574 magnitude for the gain.

575

576 **Parameters' description:**

577 **Visual familiarity directional bias:** Indicates the absolute angle away from the goal at which
578 visual familiarity signals (i.e., the CX inputs) are highest, assuming 0° indicates the correct
579 goal direction. 0° indicates that both left and right inputs fire when the nest direction is
580 aligned with the current body orientation. Inversely, 180° indicates that left and right input
581 fire when the nest is right behind. Positive values (between 0° and 180°) indicate that the
582 left and right inputs fire when the nest direction is on the left and right hand side
583 respectively (the extent of the angular bias is given by the value). Negative values (between
584 0° and -180°) indicate a reversal, so that left and right input fire when the nest direction is on
585 the right and left hand side respectively. **Visual familiarity directional noise:** Represents the
586 extent of a systematic deviation from the visual familiarity directional bias angle. It is
587 implemented by shifting the input curve response (horizontal arrows in **Fig. 1b**) around its
588 mean (given by the 'directional bias') at each time step by random values drawn from a
589 normal distribution with standard deviation given by 'directional noise'. It can be seen as
590 representing a directional noise when storing visual memories. High directional noise means
591 that the input signal will occasionally respond strongest when oriented in the other direction
592 than indicated by the visual familiarity directional bias. Robustness to visual familiarity
593 directional noise indicates that the orientation of the body does not need to be precisely
594 controlled during memory acquisition. **Motor noise:** at each time step, a directional 'noise
595 angle' is drawn randomly from a Gaussian distribution of $\pm SD = \text{motor noise}$, and added to
596 the agent's current direction. **Memory decay:** proportion of Fan-shaped Body Neurons (FBN,
597 see extended fig 2 for details) activity lost at each time step: For each FBN: $\text{Activity}_{(t+1)} =$
598 $\text{Activity}_{(t)} \times (1 - \text{memory decay})$. This corresponds to the speed at which the memory of the
599 vector representation in the FBN decays. A memory decay = 1 means that the vector
600 representation in the FBN is used only for the current time step and entirely overridden by
601 the next inputs. A memory decay = 0 means that the vectors representation acts as a perfect
602 accumulator across the whole paths (as in PI), which is probably unrealistic. **Motor gain:** Sets
603 the gain to convert the motor neuron signals (see extended fig 2 for details) into an actual
604 turn amplitude ($\text{turn amplitude} = \text{turning neuron signal} \times \text{gain}$). Note that here, the motor
605 gain is presented across orders of magnitude. One order of magnitude higher means that the
606 agent will be one order of magnitude more sensitive to the turning signal.

607 **Extended data figure 2.**



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609

610 **Extended data figure 2. Details of the CX model's circuitry.**

611 **a-d.** General scheme of the CX model as presented in figure 1 (left panel) and the
 612 corresponding detailed circuitry (right panel). This model exploits the same circuit as the CX
 613 model used for PI^{12,14}, except that FB input indicate visual familiarity rather than speed of
 614 movement.

615 **a.** Current heading direction is modelled in the Protocerebral Bridge (PB) as a bump of
616 activity across 8 neurons forming a ring-attractor (purple), as observed in insects¹⁴. Each
617 neuron responds maximally for a preferred compass direction, 45° apart from the neighbour
618 neurons (neuron 1 and 8 are functionally neighbours, closing the ring structure). Change in
619 the agent's current compass orientation results in a shift of the bump of activity across the 8
620 neurons (we did not model how this is achieved from sensory cues, see^{9,10,61} for studies
621 dedicated on this.

622 **b.** Visual familiarity signals fire according to the agent orientation relative to the goal
623 direction. Here the input curve indicates that right and left signals fire maximally when the
624 agent is oriented 50° (in average) left and right from its goal respectively (but see Fig. 1 and
625 Extended fig. 1 for variation of these parameters: 'directional bias' and 'directional noise').

626 **c.** These lateralised input signals excite two dedicated sets of FBN. These FBNs are
627 simultaneously inhibited by the current heading representation (purple), resulting in two
628 negative imprints of the current heading activity across the FBNs, which can be viewed as
629 two 'view-based vectors'. FBNs show some sustained activity so that, across time, successive
630 imprints are superimposed, thus updating the 'view-based-vectors' (as for Path integration,
631 except that this sustained activity is not crucial). The sustainability of such a 'view-based
632 vector' depends on the FBN activity's decaying rate, which can be varied in our model and
633 has little incidence on the agent's success (Extended figure 1, parameter decay).

634 **d.** Motor control is achieved using the same circuitry as for Path integration¹². On each brain
635 hemisphere, neurons (called CPU1 in some species), compare the current compass heading
636 (purple) with their version of the FBN 'view-based-vector'. Crucially, both FBN
637 representations are neurally shifted by 1 neuron (as if rotating the view-based-vector by 45°
638 clockwise or counter-clockwise depending on the hemisphere), resulting in an overall activity
639 in the CPU1 (sum of the 8 CPU1) indicating whether the view-based-vector points rather on
640 the left- (higher resulting activity in the left hemisphere) or right-hand side (higher resulting
641 activity in the right hemisphere). The CPU1 neurons sum their activity on descending motor
642 neurons (MN), which difference in activity across hemispheres triggers a left or right turn of
643 various amplitude, given a 'motor gain' that can be varied to make the agent more or less
644 reactive (Extended figure 1 for detailed parameter description). Numbers on the left indicate
645 neurons numbers. Letters on the right indicate brain areas (SIP: Superior Intermediate

646 Protocerebrum, PB: Protocerebral Bridge, FB: Fan-shaped Body, LAL: Lateral Accessory
647 Lobe).

648 **e.** Same as Fig. 4c, with added details of the PB (purple) and right and left FB (yellow and
649 orange) neural activity. Note that the FBNs order has been shifted (2,3,4,5,6,7,8,1 and
650 8,1,2,3,4,5,6,7) and inhibition exerted by the PB is represented (overlaid transparent purple,
651 1,2,3,4,5,6,7,8) as happens in the left and right CPU1 neuron (**d**). This way, the strength of
652 the motor signal for turning right and left– which correspond to the sum of non-inhibited
653 right and left CPU1 activity – can be inferred by looking at the area covered by non-occluded
654 yellow and orange FBN columns respectively.

655 With manipulation such as rotating the current compass information, it becomes apparent
656 that motor decision results from complex dynamics between two main factors: 1- how
657 strong are the left and right visual input signal updating the view-based-vectors
658 representation (represented by orange and yellow glow around the actual ant heading
659 arrows), which depend on whether the agent is oriented left or right from its goal and 2-
660 how well the current heading representation (PB) matches the rotated left and right shifted
661 FB view-based-vector current representations.

Appendix C

A killjoy perspective on object representation by bumblebees

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This appendix is published as a technical comment to:

Solvi, C., Al-Khudhairy, S. G., & Chittka, L. (2020). Bumble bees display cross-modal object recognition between visual and tactile senses. *Science*, 367(6480), 910-912.

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Technical comment to:

Solvi, C., Al-Khudhairy, S. G., & Chittka, L. (2020). Bumble bees display cross-modal object recognition between visual and tactile senses. *Science*, 367(6480), 910-912.

Title: A killjoy perspective on object representation by bumblebees

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Abstract:

Solvi et al. (*I*) reported that bumblebees trained to discriminate objects by touch could distinguish them through vision, and vice versa. We argue that this behavioural feat may be explained by egocentric heuristics rather than an abstract representation of object shapes. We call for more considerations of animals' ecology, neural circuitry and actual behaviours.

Main text:

Insect cognition research is living a golden age, with increasing numbers of studies showing that insects can solve ever more impressive behavioural tasks despite their miniature brain. In the latest example, Solvi et al. (*I*) describe an elegant experiment where bumblebees trained to discriminate cubes vs. spheres, either visually (through a transparent screen) or by touch (in the dark), could apparently also recognize them in the other modality. This suggests that insects form a “modality-independent internal representations of object shapes”, an ability that we humans are explicitly self-aware of.

This study is designed to demonstrate, in an insect, the existence of a ‘higher cognitive process’ drawn from human psychology rather than the animal’s known neuro-anatomy or natural behaviours. This approach undeniably drives the field of comparative cognition forward by suggesting unsuspected and often sensational human-like cognitive abilities in small-brained animals. However, this provides no insights on how or why these behavioural

32 feats are achieved; and because the incentive is to seek for complex phenomena, this approach
33 is subjected to the risk of overlooking more parsimonious, ‘killjoy’, explanations (2). This is
34 particularly true in insects, which perceive and interact with the world in very different ways
35 than humans do. Such an approach ought to be supplemented with considerations for
36 plausible mechanisms underlying the phenomena, ultimately enriching species comparisons
37 (3).

38 Cross-modal transfers in insects are not new (4, 5), and in some cases we have a good
39 understanding of how this is implemented in their neural circuits. For instance, insects can
40 memorise directions based on wind ,or self-motion cues perceived through mechanosensors
41 and subsequently recover these directions using visual cues (6–8). Because there is no a-priori
42 reason to link these cues in any particular fashion, such transfers require the simultaneous
43 experience of both cues at some point in the past, and involve Hebbian-like plasticity (i.e.,
44 cells that fire together wire together) in a well characterised area called the Central Complex
45 (8, 9).

46 The fascinating aspect of the new study by Solvi et al. (1) is thus not so much about a cross-
47 modality transfer per se, but the idea that such a transfer is achieved through an internal
48 representation of object shapes. This seems at odds with previous work. For instance, flies
49 (10) and bees (11) can learn to visually discriminate two triangles shown side by side, with
50 one pointing up and one pointing down, suggesting – as in the present study – their ability to
51 memorise shapes. However, this apparent ability vanishes if the triangles’ relative positions
52 are slightly shifted vertically so as to align their centres of mass, showing that insects do not
53 build a mental image of shapes, but extract instead a limited number of specific features.
54 Congruently, insects’ visual receptors and neural processing are poorly suited to reconstruct
55 the world’s shapes but remarkably efficient to pick-out task-relevant features (e.g., indicating
56 the presence of flowers in bees, flying targets in predatory insects, or distant trees in fruit
57 flies). Such filtering, so-called ‘matched-filters’, “severely limits the amount of information
58 the brain can pick up from the outside world, but frees the brain from the need to perform
59 more intricate computation to extract the information finally needed for fulfilling a particular
60 task” (12). In sum, insects seem not equipped to build internal reconstructions of the outer
61 world, but are excellent at using ecologically relevant task-related heuristics.

62 How could we reconcile Solvi et al.'s (*1*) results with such an idea? Without information
63 about the sensory-motor experience of the bumblebees, we can only provide tentative
64 explanations, more to sparkle the debate than to defend a strong belief.

65 First, bumblebees may have achieved mechano-visual associations during previous
66 experience with edges, curved or flat surfaces, presumably here also through Hebbian-like
67 plasticity. This would be exciting; however, it should be understood that such associations
68 may link egocentric perceptions (i.e., centred on the animal viewpoint rather than the world)
69 and thus do not imply any form of abstract object representation or 'world-centred'
70 reconstruction. Such egocentric cross-modal transfers would require the unimodal perception
71 to be similar to what it was during the past bi-modal experience. That is, the bumblebee
72 would need to view the object from a short distance (close enough to touch it) to trigger the
73 associated bi-modal representation.

74 Alternatively, bumblebees may have used a sensorimotor trick. Insects can visually guide
75 their legs and antennae appropriately when trying to reach an object (*13, 14*). This visual
76 control is based on egocentric features such as the apparent movement of proximal edges or
77 surfaces (*13, 14*). Therefore, even though the objects presented in Solvi et al.'s (*1*) visual
78 condition are covered with a transparent screen, bumblebees may visually adjust their
79 appendages differently when preparing to touch the round sphere or the flat, edgy cube. These
80 object-specific movements might bear similarities with the ones effected during the act of
81 sampling the objects in the dark. 'Preparing to grasp the cube using vision' and 'sampling the
82 cube in the dark' might involve similar movements, specific of the object. Because this self-
83 induced experience – whether through proprioception, motor command or both – occurs just
84 before the bumblebee receives the reward or the punishment, it is likely learnt as a salient
85 cues allowing differentiation. An operant rather than Pavlovian conditioning, which would
86 predict a spontaneous transfer across visual and dark conditions. This may sound far-fetched
87 to us humans, but it would not be the first time insects use their own movements to solve
88 object-recognition paradigms in unsuspected ways (*15*). Intriguingly, even for us, the object-
89 specific movements effected when grasping are based on a limited set of egocentric visual
90 features rather than our ability to form object-based representation (*16*).

91 In any case, both egocentric hypotheses predict that bumblebees tested in the light would need
92 to approach the object within reach to recognise it as good or bad. As it turns out, this seems
93 to be what they are doing. The example videos courteously shared by the authors showed that

94 the bumblebees tested in the visual condition approached (close enough to touch it) both the
95 rewarded and punished objects equally often (21 vs. 22 instances). Their straight approaches
96 reveal that they do see the targeted object... but have yet no information allowing
97 discrimination. The bumblebee trained in the dark further displayed multiple attempts to reach
98 the punished object through the glass with its legs or antennae before moving on. These
99 behaviours seem hard to conciliate with the psychology-inspired idea of “a complete, globally
100 accessible, Gestalt perception of the world”.

101 Surely, an analysis of the bumblebees’ actual behaviour is needed. Our egocentric
102 explanations may prove to be wrong but we hoped it showed how consideration of insects’
103 neurobiology, ecology, and sensory-motor dynamics can lead to alternative, more
104 mechanistically grounded explanations.

105

106 **References**

- 107 1. C. Solvi, S. G. Al-Khudhairy, L. Chittka, Bumble bees display cross-modal object
108 recognition between visual and tactile senses. *Science*. **367**, 910–912 (2020).
- 109 2. S. J. Shettleworth, Clever animals and killjoy explanations in comparative psychology.
110 *Trends in Cognitive Sciences*. **14**, 477–481 (2010).
- 111 3. L. Chittka, S. J. Rossiter, P. Skorupski, C. Fernando, What is comparable in comparative
112 cognition? *Philosophical Transactions of the Royal Society B: Biological Sciences*. **367**,
113 2677–2685 (2012).
- 114 4. M. Giurfa, S. W. Zhang, A. Jenett, R. Menzel, M. V. Srinivasan, The concepts of
115 “sameness” and “difference” in an insect. *Nature*. **410**, 930–933 (2001).
- 116 5. D. A. Lawson, L. Chittka, H. M. Whitney, S. A. Rands, Bumblebees distinguish floral
117 scent patterns, and can transfer these to corresponding visual patterns. *Proceedings of*
118 *the Royal Society B: Biological Sciences*. **285**, 20180661 (2018).
- 119 6. A. Wystrach, S. Schwarz, Ants use a predictive mechanism to compensate for passive
120 displacements by wind. *Current biology: CB*. **23**, R1083–R1085 (2013).
- 121 7. M. Dacke, A. T. Bell, J. J. Foster, E. J. Baird, M. F. Strube-Bloss, M. J. Byrne, B. El
122 Jundi, Multimodal cue integration in the dung beetle compass. *Proceedings of the*
123 *National Academy of Sciences*. **116**, 14248–14253 (2019).
- 124 8. S. S. Kim, A. M. Hermundstad, S. Romani, L. F. Abbott, V. Jayaraman, Generation of
125 stable heading representations in diverse visual scenes. *Nature*. **576**, 126–131 (2019).
- 126 9. A. Honkanen, A. Adden, J. da S. Freitas, S. Heinze, The insect central complex and the
127 neural basis of navigational strategies. *Journal of Experimental Biology*. **222**, jeb188854
128 (2019).

- 129 10. R. Ernst, M. Heisenberg, The memory template in *Drosophila* pattern vision at the flight
130 simulator. *Vision Research*. **39**, 3920–3933 (1999).
- 131 11. A. Horridge, Two-dimensional pattern discrimination by the honeybee. *Physiological*
132 *Entomology*. **24**, 197–212 (1999).
- 133 12. R. Wehner, ‘Matched filters’ — neural models of the external world. *Journal of*
134 *Comparative Physiology A*. **161**, 511–531 (1987).
- 135 13. R. E. Ritzmann, A. Büschges, Adaptive motor behavior in insects. *Current Opinion in*
136 *Neurobiology*. **17**, 629–636 (2007).
- 137 14. C. Evangelista, P. Kraft, M. Dacke, J. Reinhard, M. V. Srinivasan, The moment before
138 touchdown: landing manoeuvres of the honeybee *Apis mellifera*. *Journal of*
139 *Experimental Biology*. **213**, 262–270 (2010).
- 140 15. M. Guiraud, M. Roper, L. Chittka, High-speed videography reveals how honeybees can
141 turn a spatial concept learning task into a simple discrimination task by stereotyped
142 flight movements and sequential inspection of pattern elements. *Frontiers in psychology*.
143 **9**, 1347 (2018).
- 144 16. D. Milner, M. Goodale, *The visual brain in action* (OUP Oxford, 2006), vol. 27.
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AUTHOR: Florent Le Moël

TITLE: *Visual navigation in ants: a modelling approach*

THESIS SUPERVISOR: Antoine Wystrach

DEFENSE DATE AND LOCATION: July 27, 2021 - 4R4 building Conference Room, Paul Sabatier University

SUMMARY:

The study of insect navigation has been benefitting from both a rich history in ethology and sensory physiology, and from the recent advances in neurobiology and neuroanatomy. However, it remains difficult to establish direct links between the identified neural circuits and the behaviour, and this is often not sufficient to reach a true understanding of the complex dynamics involved. For this, it is necessary to formulate hypotheses in a theoretical framework, and modelling is an excellent tool for this. This thesis presents such a modelling approach, presenting simulations and computer models of several brain structures involved in navigation in the ant. All the models described here have the common aim to contribute to our global understanding of navigation in the insect: they seek to reproduce experimentally observed behaviours, and they are strictly bio-plausible in their implementation.

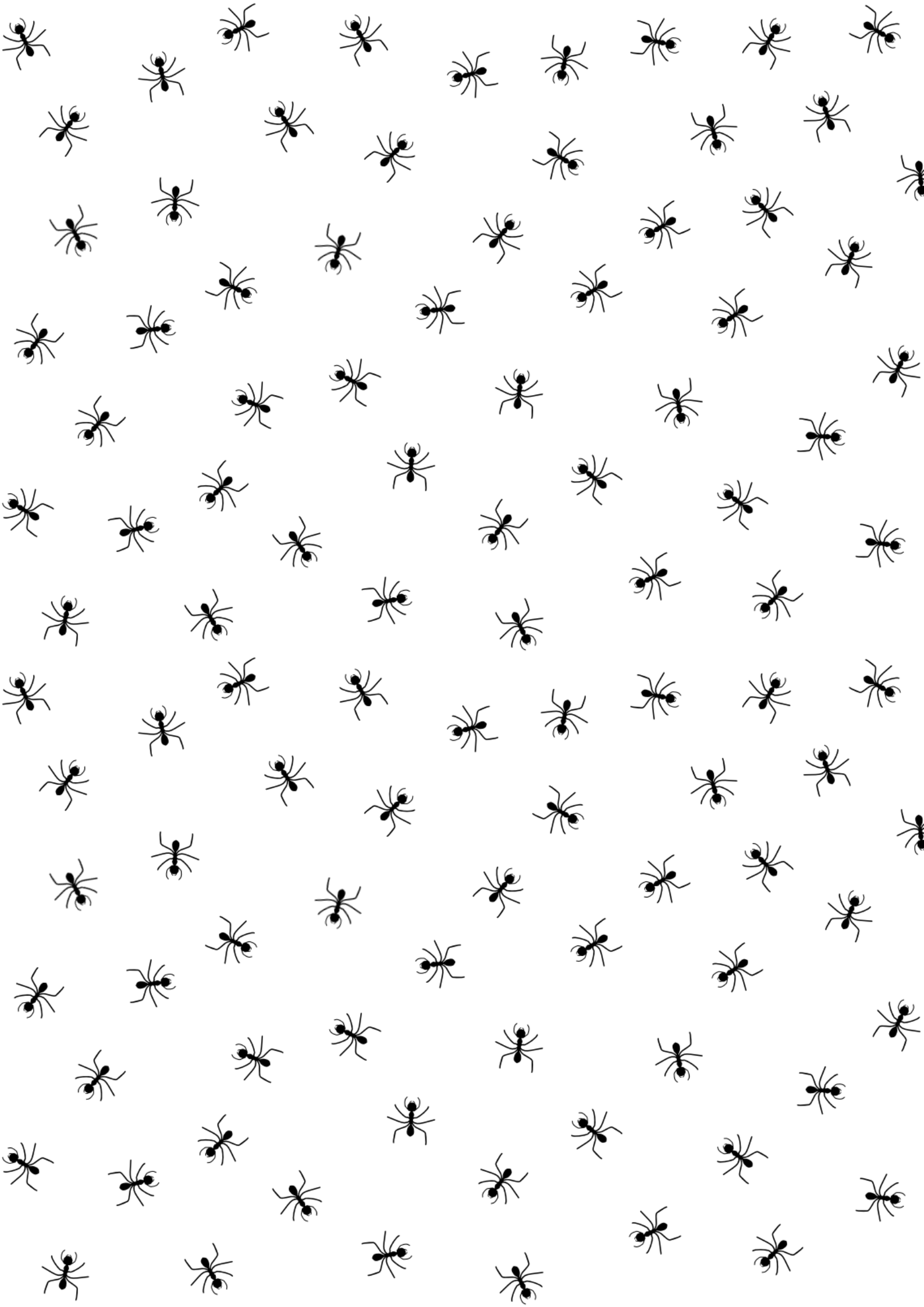
KEYWORDS: neuroethology, insect, behaviour, navigation, ant, cataglyphis, computational, modelling, bio-inspired, simulation, central complex, mushroom bodies

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SPECIALITY: Neurosciences

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TITRE : *Navigation visuelle chez la fourmi : approche modélisatrice*

DIRECTEUR DE THÈSE : Antoine Wystrach

LIEU ET DATE DE SOUTENANCE : 27 Juillet 2021, Salle de Conférence du bâtiment 4R4, Université Toulouse III Paul Sabatier

RÉSUMÉ :

L'étude de la navigation chez l'insecte bénéficie à la fois d'un riche historique en éthologie et physiologie sensorielle, et des récents progrès en neurobiologie et neuroanatomie. Mais il reste cependant difficile d'établir des liens directs entre les circuits neuronaux identifiés et le comportement, et cela ne suffit souvent pas pour parvenir à une véritable compréhension des dynamiques complexes qui sont en jeu. Pour cela, il est nécessaire de formuler des hypothèses dans un cadre théorique, et la modélisation représente pour cela un excellent outil. Cette thèse présente une telle approche modélisatrice, présentant simulations et modèles informatiques de plusieurs structures cérébrales impliquées dans la navigation chez la fourmi. Tous les modèles décrits ici ont comme but de participer à notre compréhension globale de la navigation chez l'insecte: ils cherchent à reproduire des comportements observés expérimentalement, et sont strictement bio-plausibles dans leur implémentation.

MOTS-CLÉS : neuroéthologie, insecte, comportement, navigation, fourmi, cataglyphis, modélisation, informatique, bio-inspiré, simulation, complexe central, corps pédonculés

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