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Essay

What can we learn from studies of insect navigation?

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The remarkable navigational abilities of social insects are proof that small brains can produce exquisitely efficient, robust navigation in complex environments. Because social insects produce specialist foragers that are amenable to field and laboratory studies, they have been productive model systems for studies of navigation. Ideas derived from these studies of insect navigation have shown how simple mechanisms can produce robust and seemingly complex behaviour. This is important for a general understanding of spatial cognition as these 'insect-like' navigational behaviours are probably phylogenetically widespread. Current insect research is helping to show how simple panoramic views, without the need for cognitive processes such as object identification or labelling, can provide explanations for many findings, including behaviours that in the vertebrate literature have traditionally drawn conclusions about sophisticated high-level spatial modules or learning rules. Recent insect navigation research has only been possible because of techniques enabling the recording of visual scenes from the perspective of the insect. Without such techniques one has to intuit an animal's point of view (its Umwelt) and we discuss how this may lead to unhelpful assumptions about the cues available for navigation.

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A major goal within biology and psychology is to understand the intelligence of animals. For many, this field of animal cognition is concerned with investigating the development and precursors of seemingly unique human intelligences (de Waal & Ferrari 2010). However, a more general project is to examine the similarities and differences between species in their cognitive solutions to day-to-day tasks. This helps us understand how animal intelligence depends on factors such as environment, social structure, evolutionary history and brain size. From *Aplysia* to humans, we see many similarities in neural hardware, from the nature of action potentials to the mechanisms of memory (Kandel et al. 2000). There is therefore no a priori reason why we should not also see phylogenetically widespread cognitive strategies when we look at animals' solutions to similar problems (Shettleworth 2010a). In this context, investigations of well-defined behaviours, such as navigation, provide an ideal ground for questions of comparative cognition.

Using learnt information to navigate within a familiar environment undoubtedly solicits several cognitive processes. An animal must extract from its environment the information that is relevant to navigation and robustly organize this into memories. Then, when navigating, it must convert those memories into spatial decisions.

Navigation has major advantages as a model behaviour for comparative cognition as it is a universal behaviour: most animals have to solve the problem of navigating to important locations. Second, the goal of a navigating animal, getting from A to B, is a clearly defined spatial behaviour that produces a low-dimensional behavioural output (movement in space and time) which can be objectively quantified by scientists. For comparison, consider the study of communication. In this case, both the intention of the signaller and the nature of the communication channel are opaque to a third-party observer, and it may take considerable effort just to decipher the function of a signal.

In this essay we consider how studies of insect navigation can illuminate the field of spatial cognition by complementing a bottom-up approach to comparative cognition. Studies of insects can help us to understand the basic navigational toolkit that is likely to be phylogenetically widespread and the robust, seemingly complex, navigational behaviour that can be achieved with it.

A BOTTOM-UP PERSPECTIVE ON SPATIAL COGNITION

A basic difficulty within animal cognition research comes from attempts to infer mental processes and neural mechanisms from observations of behaviour. For instance, watching a dog bounding towards his master, or a rat pressing a lever to get food, may lead to conclusions about the dog's love for his master or the rat's understanding of the mechanisms of a Skinner box. A long-held principle

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within the field that is meant to guard against such anthropomorphic attributions is known as Morgan's Canon:

In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development. (Morgan 1903, page 59)

It is hard to apply Morgan's Canon formally in modern science because of the near impossibility of developing watertight definitions of higher and lower psychological processes. However, it is an important shared reference because most scientists hold a common sense intuition about the sensible and valid inferences one can make from behavioural observations, and thus the spirit of Morgan's Canon is alive. This spirit incorporates the general principle of parsimony, which permeates all science, as well as an evolutionary perspective on cognition. Such a way of thinking prompts us to consider how cognitive adaptations must have evolved from more basic, phylogenetically widespread processes. This spirit of Morgan's Canon is evident in bottom-up perspectives on animal cognition (Shettleworth 2010b; de Waal & Ferrari 2010). This view of animal cognition asks questions such as 'To what extent can complex behaviours be explained by simple cognitive mechanisms?' and 'how might species-specific cognitive adaptations depend on common fundamental processes?'

When studying spatial cognition, a bottom-up perspective involves considering how basic, phylogenetically widespread, spatial mechanisms, such as simple orientation reflexes and taxes, might underpin more complex behaviours such as piloting and route learning, and to what extent these navigational strategies can account for seemingly complex behaviour. A preliminary theoretical consideration of such a hierarchy, from taxis behaviours all the way to uniquely human spatial abilities, such as map reading and verbal accounts of space, is provided by Wiener et al. (2011).

Within insect navigation research, a heritage of sensory physiology has promoted a bottom-up approach (Cartwright & Collett 1983; Wehner & Wehner 1986, 1990; Wehner 1994, 2003; Srinivasan et al. 1996, 2000). It is our goal with this essay to show how studies of insect navigation have given us a detailed mechanistic understanding of basic navigational strategies. The applicability of this research to general spatial cognition comes from asking how much of navigational behaviour can be explained by 'insect-like' strategies.

INSECT NAVIGATION

The remarkable navigational abilities of social insects are proof that small brains can produce exquisitely efficient, robust navigation in complex environments (Menzel & Giurfa 2001; Wehner 2003; Srinivasan 2010). We know a relatively large amount about the cognitive abilities of insects because social insects are particularly easy to study, especially when it comes to navigation. The eusocial organization of a colony means that there are individual specialist foragers, who have to return home repeatedly to be successful. With these dedicated foragers, it is easy to assign the correct motivation to their behaviour, and they can be easily monitored outdoors (Santschi 1913; von Frisch 1967; Wehner 1972; Collett & Land 1975), where we can assess the available sensory information (Zeil et al. 2003; Stürzl & Zeil 2007; Towne & Moscrip 2008; Philippides et al. 2011). By sketching the career of an individual forager, we can see how, for social insects, robust behaviour comes from the adaptive integration of innate strategies and learning.

Upon first leaving the nest or hive, a new forager performs a 'learning walk' or 'learning flight', where a carefully orchestrated series of loops and turns allows her to learn the visual surroundings from perspectives that will be useful on subsequent return journeys

(Zeil 1993a, b; Wehner et al. 2004; Hempel de Ibarra et al. 2009; Müller & Wehner 2010). Then, when the forager finally leaves the vicinity of the nest to forage, she is safely connected to it because of her path integration (PI) system. With PI, odometric and compass information are continuously combined such that at all times during a journey the forager has the approximate direction and distance information required to take a direct path home (Wehner & Srinivasan 2003; Ronacher 2008). By remembering the coordinates of a successful foraging patch, the forager can also use PI to chart food-bound routes (Wehner et al. 1983; Schmid-Hempel 1984; Collett et al. 1999) or pass information to nestmates (von Frisch 1967). PI is subject to cumulative error and does not register passive displacements, such as those caused by a gust of wind. To mitigate these risks, foragers learn the visual information required to guide routes between the colony and their foraging grounds. Ultimately, for experienced foragers, the information provided by visual scenes dominates the information given by PI in cases of conflict (von Frisch 1967; Collett et al. 1992, 1998; Andel & Wehner 2004; Kohler & Wehner 2005; Narendra 2007; Graham & Cheng 2009; Reid et al. 2011), but PI continues to operate in the background (Collett et al. 1998; Andel & Wehner 2004; Collett & Collett 2009) as a safety net.

This simple sketch of the life of a forager tells a nice story of how robust navigation comes from the interaction of innate behaviours (such as PI and learning walks) and learnt (mainly visual) information. In the next section we consider some aspects of insect navigation in more detail, with two well-studied topics that have helped us to understand the style of cognition insects use for navigation.

INSECT NAVIGATION: HISTORICAL LESSONS

As discussed above, there are practical benefits of working with social insects and these have enabled us to gain a deep understanding of the behavioural repertoire underpinning navigation in these industrious foragers. For the purposes of this essay, we want to focus on what we have learnt about the cognitive mechanisms behind insect navigational behaviour, and then consider those mechanisms with respect to the navigation of other animals. In this regard, two historical examples are informative, both as demonstrations of how controlled behavioural experiments can elegantly uncover low-level mechanisms and as exemplars of how studies of insects can lead to parsimonious explanations of seemingly complex navigational behaviour.

Navigation by Simple Views

Niko Tinbergen demonstrated in his famous digger wasp experiment the importance of visual information for navigation (Tinbergen & Kruyt 1938). Tinbergen identified a digger wasp nest and placed a ring of pine cones around the entrance. When the digger wasp departed, she inspected the nest surroundings before leaving on her foraging trip. While the wasp was away, Tinbergen relocated the pine cone ring. On her return the wasp searched at the centre of the relocated pine cone ring even though the real nest entrance was only centimetres away. Following Tinbergen, experiments with hoverflies (Collett & Land 1975), desert ants (Wehner & Rüber 1979), honeybees (Cartwright & Collett 1983) and even waterstriders (Junger 1991) have all suggested that insects store the visual information required to return to a goal, as an egocentric view of the world as seen from that place. The Cartwright & Collett (1983) experiments are the paradigmatic experiments of this type. Honeybees were trained to find a sucrose feeder at a position defined solely by simple black cylinders in an otherwise plain room. In probe tests, with no feeder present, bees' search distributions were recorded.

Overall, after tests with different-sized cylinders, and cylinders in different configurations, bees' searches were best explained by bees searching at a location where the world had the most similar appearance to that experienced from the feeder during training. A series of modelling experiments showed how this behaviour could be implemented by minimizing the difference between the current view of the world and the remembered view from the feeder. Following Cartwright & Collett, a large volume of research has focused on the use of egocentric views for navigation in animals and robots. Collectively, these theories and models are referred to as 'view-based matching' strategies.

There are two functionally distinct ways of using stored views to generate spatial behaviour. The classic Snapshot model (Cartwright & Collett 1983) and derivatives (Franz et al. 1998; Lambrinos et al. 2000; Zeil et al. 2003; Vardy & Möller 2005; Möller & Vardy 2006) treat a single view as an attractor, which can be approached from any direction. An alternative use of a stored view is as a visual compass (Zeil et al. 2003; Graham et al. 2010; Wystrach et al. 2011a; Baddeley et al. 2012). Here comparisons between current view and stored view can be used to recapture the orientation the animal had at the time the view was stored.

Thus, stored views can be used to home to a point or set a direction, two actions that are fundamental components of navigation for any animal. What's more, there are fundamental reasons why view-based matching is a sensible, efficient strategy for any navigator. For animals with any type of visual system, view-based matching is a computationally inexpensive process because information about the world is stored in an egocentric frame of reference. The agent is therefore freed of any complex allocentric representation and does not have to undertake the computations required to move information between different coordinate schemes. This is possible because an egocentric view is an excellent task-specific representation of the world. Movements in space (i.e. navigational behaviour) map simply onto changes in the position of visual components of a view; moreover, errors between current views and remembered views can be simply transformed into corrective rotations or translations.

Because of the ontogeny of the idea and the parsimony of the algorithm, the use of egocentric remembered views for navigation is often thought (perhaps pejoratively) as an insect solution. The truth is that animals unavoidably deal with egocentric views, as their visual input is by definition egocentric and our key point here is to emphasize how egocentric views provide effective and economical solutions for navigation. Therefore it is no surprise that we see convergent use, across the animal kingdom, of egocentric views for spatial tasks (Roskoss-Ewoldsen et al. 1998; Wang & Spelke 2002; McNamara 2003; Shelton & McNamara 2004; Pecchia & Vallortigara 2010; Pecchia et al. 2011). We discuss later how a developing understanding of the power of egocentric views (particularly panoramic views) is opening new lines of discussion around classic vertebrate experimental paradigms.

The Organization of Spatial Memories

Simple views are a robust way of recognizing a familiar location, setting a heading or even guiding oneself to a discrete goal, that is, undertaking the basic components of navigation. But the behaviour of mature foragers demonstrates that an insect's world knowledge must be composed of a very extensive set of spatial memories in order to guide foraging routes. One of the most persistent debates within navigation research is how animals organize these memories. Particular attention is routinely paid to whether animals organize memories into a single representation of the world: a so-called 'cognitive map' (Tolman 1948). There is debate regarding the precise definition of the term (Gallistel 1989; Bennett 1996; Cruse &

Wehner 2011; Wiener et al. 2011) and indeed there is debate over whether the term can even be usefully defined (Bennett 1996). However, we can side-step the problem of defining a cognitive map and still ask sensible questions about the organization of spatial memories. Solitary foraging ants are particularly useful in this regard, as we can observe the lifetime's work of a forager in her natural habitat with nothing more technical than a pencil and paper. Here we consider three types of behavioural experiments with ants that are insightful regarding the way that they organize spatial memories.

(1) One common question is to ask whether the organization of an animal's spatial memories allows for ants to take novel routes to familiar locations, without these novel routes being guided simply by PI or view-based homing. While there are lots of examples of novel routes in ants released at novel locations (e.g. Wehner et al. 1996; Durier et al. 2004; Narendra 2007) all the documented cases can be explained by the application of the same visual route memories that ordinarily guide habitual routes (Collett et al. 2007). This is possible because of the informational content of natural visual scenes. A stored view that may be used to guide a portion of a habitual route will contain information from objects at a variety of scales and distances. Even in novel locations, large features that appear in en route views will be part of the scene and can often underpin sensible headings for the novel location. The lesson here is that the basic properties of natural images, whereby information is available at multiple scales, means that the use of egocentric views for navigation is a robust mechanism. We should note that the issue of novel routes in honeybees is less clear. Gould's (1986) original observation of novel routes could not be replicated (Wehner & Menzel 1990; Dyer 1991). However, novel routes have since been observed using radar (Menzel et al. 2005; Menzel et al. 2011), although the data are limited and not yet conclusive.

(2) Holding spatial information in a shared representation, such as a cognitive map, might suggest that information usually implemented in one behavioural context could be accessed in a different behavioural context. For ants, an elegant experiment by Wehner et al. (2006) shows how information used in different contexts is in fact insulated. Using barriers, the researchers were able to separate 'foodward' and 'nestward' routes spatially so that the entire foraging journey formed a looped path. Experienced ants on their inbound route were captured from the feeder or near the nest and then displaced to a point on their habitual outward route. Despite this being a familiar location, ants behaved as if at a novel location and only managed to return home when their search led them to their familiar inbound route. The use of contextual information to prime and insulate route memories (Collett et al. 2006) allows for a certain behavioural flexibility, as specific routes can be associated with variables such as satiety level (Harris et al. 2005), time of day (Moore et al. 1989) or, for honeybees, odours introduced to the hive by returning foragers (Reinhard et al. 2004). But, as shown by Wehner et al. (2006), it can also constrain the use of spatial memories.

(3) A third property of ant behaviour that has been thought of as evidence for a cognitive map is the binding of information from different navigational modalities. For instance, the PI system would allow coordinates to be allocated to key goals and landmarks so that locations would share a common frame of reference. There is evidence of an indirect interaction between view learning and PI. For instance, PI can be used to align the body towards the nest direction when learning relevant homing views (Müller & Wehner 2010). However, there is no evidence that familiar locations or prominent landmarks can become associated with the metric information acquired from PI (Collett et al. 2003; Knaden & Wehner 2005; Collett & Collett 2009; Cruse & Wehner 2011).

Overall, the absence of any behavioural signatures that would indicate cognitive maps in ants may be used as evidence that they

do not possess the neural and cognitive sophistication to implement cognitive maps. However, we would like to stress a different point. Let us not forget that ant navigational performance is exceptional and the extensive world knowledge of experienced foragers is manifest in idiosyncratic routes (Graham et al. 2003; Kohler & Wehner 2005; Macquart et al. 2006; Collett 2010). Idiosyncratic habitual routes, such as those taken by ants, are also observed in vertebrates (Calhoun 1962; Hartley et al. 2003; McNamara & Shelton 2003; Biro et al. 2004; Meade et al. 2005) and seem to be a convergent strategy for moving through familiar environments, something similar to our common experience of recapitulating a well-known route on 'autopilot'. Route following in ants can be achieved by simply keeping oriented in the direction that presents the most familiar view (Collett 2010; Wystrach et al. 2011a,b,c, 2012; Baddeley et al. 2012). This coincides well with evidence in humans showing that recognition of views along a route is dependent on egocentric orientation (Shelton & McNamara 2004). Thus we see convergent behaviours across taxa for robust and economical navigational strategies. Studies of insects, especially ants, promise to get at the details of how habitual routes are learnt and controlled.

INSECT NAVIGATION: A CURRENT QUESTION

The examples in the previous section are demonstrations of how simple mechanisms can account for complex behaviour: a bottom-up perspective. A large part of the navigational toolkit discussed in those examples involves the smart use of visual information. This is reflected in aspects of current insect navigation research, where the focus is on what information is available to an insect's panoramic visual system and how that information is used. Bottom-up approaches here require an objective quantification of the information available to the animal, which can be achieved, in the case of insect vision, by recording and analysing 360° pictures of the environment (Zeil et al. 2003). Being able to consider visual tasks from the perspective of the animal reduces the chances that the perception of a human experimenter will bias the interpretation of an experiment. We illustrate this point with an example of one of our own recent experiments.

The Power of Simple Panoramic Views

Ants were trained to find their nest in front of a large high-contrast landmark (3 m wide and 2 m high). The landmark stood in an area cleared of natural clutter and devoid of other proximal landmarks so that it seemed prominent, and very useful for guiding returns to the nest. To humans observing the landmark, it would seem an obvious cue to use (Fig. 1). Yet, small displacements of the landmark revealed that, surprisingly, ants did not aim towards it in order to return to their nest. This result becomes much less surprising as soon as one examines images of the scene taken from an ant's point of view. The landmark is far less significant than it appears to a human observer (Fig. 1). The results of this experiment (Wystrach et al. 2011c) and other recent experiments in natural visual environments (Graham & Cheng 2009; Wystrach et al. 2012) suggest that navigation is based on scene recognition, and does not require the extraction and identification of landmarks. In these cases, because we have been able to analyse panoramic images taken from an ant's perspective, we have been able to explain most aspects of the ants' behaviour with parsimonious mechanisms that do not rely on the identification of specific landmarks.

Ants may not focus on individual landmarks, even seemingly obvious ones, but appear to be guided instead by information from panoramic scenes that encompass both proximal and distant cues, without functionally labelling specific landmarks. In natural



Figure 1. Human and ant perspectives. The two images are taken from the same location close to an experimental set-up, which includes a large black object. The upper image represents a human perspective and the lower image represents an ant's perspective. The ant's perspective is achieved by taking a panoramic image with lowered resolution to match the visual acuity of ants. The vertical black lines in the ant's perspective image delimit the field of view of the 'human' picture.

conditions, panoramic views encompass distant cues, such as hills or prominent trees, so that view-based matching strategies become remarkably robust when based on panoramic views of outdoor scenes (Zeil et al. 2003; Mangan & Webb 2009). Simple panoramic view matching explains route following well (Wystrach et al. 2011a, 2012; Baddeley et al. 2012) as well as the many instances of ants and bees being able to home from novel release points (Santschi 1913; Fourcassié 1991; Wehner et al. 1996; Menzel et al. 1998; Capaldi & Dyer 1999; Collett et al. 2007; Narendra 2007; Pahl et al. 2011; Wystrach et al. 2012), or successfully use skylines (Fukushi 2001; Graham & Cheng 2009) or dim scenes during twilight (Reid et al. 2011) for navigation.

Even in experiments in which artificial landmarks are made prominent and other cues minimal, some results hint at the use of inclusive panoramic views. For example, wood ants trained to follow a single conspicuous black bar moving on an LCD screen presented a small bias, revealing that they were also guided by other static visual features of the arena (Lent et al. 2009). Similarly, ants used to aiming first at a conspicuous black cylindrical landmark before turning towards the food source continued to display such a detour when the landmark was removed and their starting position displaced (Graham et al. 2003). In this case, as in others (Wystrach 2009; Wystrach & Beugnon 2009), ants proved able to navigate robustly using the visual information provided by seemingly plain experimental arenas. Using simple panoramic views, rather than focusing on isolated landmarks, seems an appropriate strategy to cope with the complexity of natural scenes and the poor resolution of insects' eyes.

The Experimenter's Visual Umwelt (and their assumptions)

The concept of a landmark is a good example of how human descriptions of the world can influence the way experiments in animal navigation are designed and interpreted. Humans find it elementary and obvious to identify landmarks, but primates have evolved an entire specialized stream dedicated to object recognition (Mishkin et al. 1983; Goodale & Milner 1992). For us, a scene is explicitly constituted of definite elements that can be individually identified and labelled with names such as 'tree', 'black cylinder' or 'wall'. Such labelling results from visual information supplied by a high-resolution fovea, on top of which are added multiple stages of visual and cognitive processing. All this processing delivers our visual Umwelt (self-world): our personal way of seeing the world resulting from filters developed during our evolutionary and personal history

(von Uexküll 1957). As we showed above, with an example from our own work, one has to guard against the biases in experimental design and interpretation that might arise from our human Umwelt.

When Tinbergen discovered that displacing a circle of pine cones, which had surrounded a digger wasp burrow, would lure the wasp into searching for its burrow within the displaced pine cones, it appeared reasonable to conclude that the wasp's homing was controlled by these 'nearby landmarks' (i.e. the pine cones). However, it is anthropocentric to think that the wasp was using those pine cones as labelled landmarks for guidance, while filtering out the rest of the panorama. As supported by the examples above, it is more likely that the insect's final approach was guided by the whole scene, within which proximal objects dominate because their image on the retina changes significantly with displacement.

Many studies show clearly that insects are strongly influenced by objects that we can label, such as trees (Santschi 1913; von Frisch 1967; Fourcassié 1991), bushes and stones (Wystrach et al. 2011b), black cylinders (Wehner & Räber 1979; Cartwright & Collett 1983; Graham et al. 2003; Narendra 2007; Collett 2010) or walls (Graham & Collett 2002; Harris et al. 2005; reviewed in Collett et al. 2006, 2007). But we did not find a single one of those results that could not be explained parsimoniously by the use of simple views, and that does not require us to invoke the ability of insects to identify individual landmarks. One might even go so far as to suggest that the use of the word 'landmark', in referring to the cues that animals might use, should be avoided. It creates a top-down bias about what information we expect animals to use in a given experiment. This stems from our way of seeing, rather than from direct evidence. Bottom-up experimental techniques, such as the use of objective panoramic pictures and measurements of the insect's visual anatomy, provide a more reliable insight into an animal's Umwelt, rather than starting with our own Umwelt.

LANDMARKS OR SCENES FOR VERTEBRATES?

Inspired by research in insect navigation, navigational models have shown that robust and accurate navigation in natural environments can be achieved with a simple ability to store and recognize scenes (Zeil et al. 2003; Möller & Vardy 2006; Baddeley et al. 2012). For robust scene recognition, what matters is the spatial arrangement of the objects across the scene, and not the identification of specific individual objects, which in natural environments might appear very similar. After all, the ability to recognize an object independently of its visual surroundings is necessary only if that object can be displaced and needs to be recognized in various locations, which by definition makes the object unreliable for navigation. Therefore we can wonder why animals would accept the processing cost of isolating and recognizing individual objects for navigational purposes, when simple egocentric views can encompass the overall structure and layout of a scene and underpin economical and robust navigation (Benhamou 1998; Zeil et al. 2003; Collett 2010; Graham et al. 2010; Philippides et al. 2011; Baddeley et al. 2012; Wystrach et al. 2012).

In fact, we see behavioural evidence that rats, as do insects, spontaneously rely on landmark configuration rather than landmark identity for navigation (Benhamou & Poucet 1998). Vertebrates, in general, may still use objects within experiments as individually recognized landmarks (Brown et al. 2010), but we should be cautious, as object recognition could well be a by-product of non-navigational processes. For instance, object and spatial memories seem to be dissociated in rat (Winters et al. 2004) and primate brains (Alvarado & Bachevalier 2005; Bachevalier & Nemanic 2008). In primates, the ventral stream that allows object recognition appears to have evolved for reasons other than spatial navigation. For example, human patients with visual agnosia

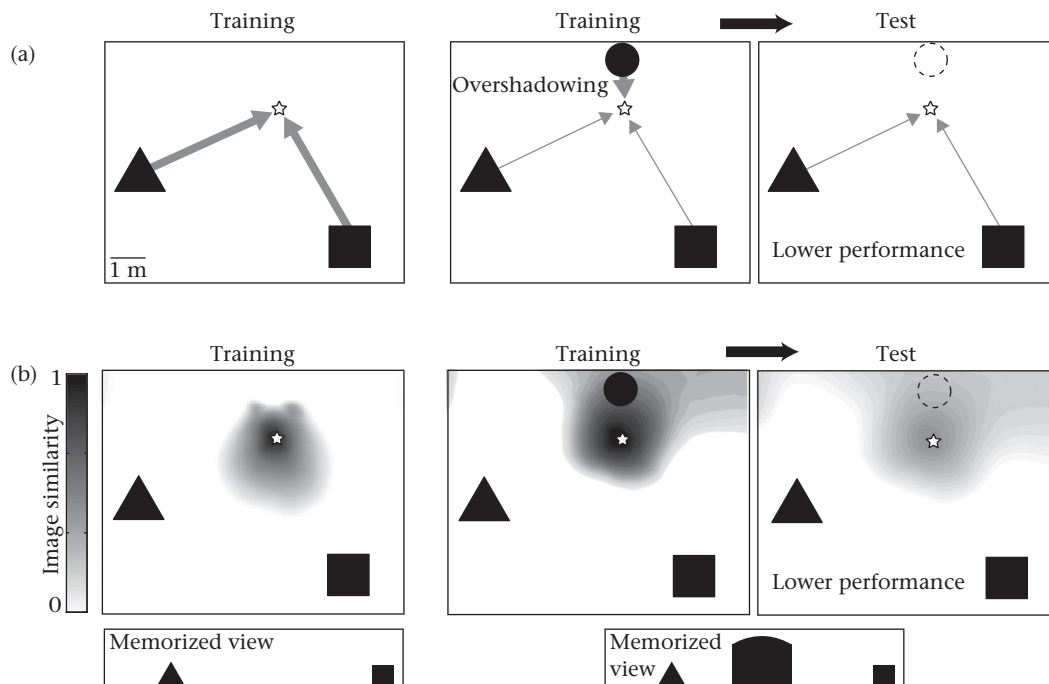


Figure 2. Explanations of landmark overshadowing. Animals can learn to pinpoint a goal in the presence of two or three landmarks. With three landmarks, if the closest landmark to the goal is removed after training, pinpointing accuracy drops. This response can be explained in two ways. (a) The animal has associated each landmark with a vector (grey arrows) pointing towards the goal (star). Stronger weights (arrow thickness) are given to landmarks that are closer to the goal (Cheng 1988). The presence of a third landmark, close to the goal during training, induces weaker weights for the two other landmarks, a concept called overshadowing. This explains why performance drops if the third landmark is removed (dashed circle) during tests (right). (b) It could be supposed that the animal has memorized the view perceived at the goal, and uses this memory to search for the goal (star). Analysis of the similarity between a view stored at the goal and panoramic pictures from other locations shows how search guided by views would explain the performance predicted by overshadowing. In these panels darker areas represent locations where a better match is possible with the goal view. In tests (right) with the closest landmark removed (dashed circle) the grey shading indicates that it is not possible to get a good match.

following brain damage in the ventral stream are often unable to recognize objects, even though they can navigate through the world with considerable skill (Farah 1990). In contrast, spatial navigation can be strongly impaired when lesions occur in the parahippocampal place area. This region is involved in scene recognition, based on wide-field visual input, and treats scenes in a unified way, independently of the component elements (Epstein 2008). Thus, as for insects, aspects of human navigation may be dependent on wide-field encoding of scenes.

Widespread through the vertebrate literature there are assumptions about the use of individual landmark identification or functional segregation between landmarks and background (reviewed in Tommasi et al. 2012). We believe that parsimonious explanations based on panoramic visual input are worth considering. For example, Fig. 2 shows how view-based matching may account for behavioural results that are usually explained by theories assuming individual landmark recognition, such as landmark–vector associations (Cheng 1988), or the application to spatial cognition of the learning theory concept of overshadowing (Pavlov 1960).

Another extant debate of this type involves experiments investigating animals' apparent use of geometrical cues. Vertebrates have been assumed to segregate functionally the geometrical layout of the environment from the features that compose it (Cheng 1986; Cheng & Newcombe 2005). The topic has been controversial (Cheng 2008), with some experiments suggesting that behaviour could be explained by feature-based mechanisms (Pearce et al. 2004, 2006). However reports of the extraction of geometrical cues are widespread (Cheng & Newcombe 2005). Here also, a bottom-up approach has provided a more parsimonious explanation. By quantifying, for the first time, the available visual information in rectangular environments, Stürzl et al. (2008) showed that the geometrical shape of arenas is implicitly contained in panoramic views and that simple view-based strategies can explain the results obtained with vertebrates (Cheung et al. 2008). When ants are tested in rectangular arenas similar to those used in the classic rat experiments they also show the same characteristic disorientation (Wystrach & Beugnon 2009). Of course, for insects, an explanation based on simple views is more readily accepted. So, after two decades of experiments in rectangular arenas, the potential role of egocentric panoramic views is being taken seriously and, recently, direct evidence for such use of egocentric views has been found in ants (Wystrach et al. 2011a) as well as in birds (Pecchia & Vallortigara 2010; Pecchia et al. 2011).

CONCLUSIONS

Our aim here was to show how studies of insect navigation could be a useful complement to a bottom-up philosophy of comparative cognition. Studies of navigation are interesting in this respect because navigation is an easy to study, universal behaviour, and the ease of working with social insects means we have been able to gain a deep understanding of their navigational mechanisms. Insect and vertebrate navigational behaviours show significant convergence, for example PI, stereotypical route following, homing from novel release points, or characteristic disorientation in a rectangular arena.

Explanations of insect spatial behaviour have usually been unburdened by assumptions about higher-level cognitive processes. This has led to the discovery of simple mechanisms, such as using egocentric views without identifying individual landmarks. These mechanisms allow for efficient, robust and flexible navigation in complex natural environments (Zeil et al. 2003; Collett 2010; Graham et al. 2010; Philippides et al. 2011; Baddeley et al. 2012; Wystrach et al. 2012). There is an ever-growing body

of evidence that navigational behaviour in vertebrates, including humans, may also arise from simple mechanisms based on egocentric views (Shelton & McNamara 1997; Roskos-Ewoldsen et al. 1998; Wang & Spelke 2002; Cheng 2008; Platt & Spelke 2009; Sheynikhovich et al. 2009; de Waal & Ferrari 2010; Pecchia & Vallortigara 2010; Pecchia et al. 2011). We believe that this convergence justifies a continued interest in considering insect navigation research as a natural bed-fellow for a bottom-up perspective on animal cognition.

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