

Comparative Approaches to Human Navigation

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Introduction

When we reflect on human spatial abilities, we are apt to be struck by the feats of geographers, who chart the earth far beyond the bounds of any person's unaided locomotion and construct accurate and detailed maps of the terrain. Although most humans are not professional geographers, intuition suggests that all human navigation depends on a version of the geographer's charts: an internal, enduring, allocentric, and unitary "cognitive map" of the environment through which we travel. Surprisingly, however, studies of animal navigation suggest that this intuition is wrong. The fundamental spatial representations underlying navigation in animals as diverse as ants, fish, rodents, and primates are dynamic rather than enduring, egocentric rather than allocentric, and encapsulated with respect both to their inputs (which constitute a restricted subset of the environmental information that animals detect) and outputs (which constitute a restricted subset of the actions and computations that animals perform). Moreover, recent studies suggest that, contrary both to intuition and to longstanding theories in human cognitive psychology, these same spatial representations also are fundamental to human navigation. The rich research traditions in behavioural ecology and comparative psychology may be better guides than human intuition to theories of human spatial performance.

The relationship between human and animal studies is not, however, a one-way street, for studies of human navigation can provide methodological and theoretical insights into the mechanisms of navigation in non-human animals. Here we review research on three systems which, we believe, are especially fundamental to human and animal navigation, and for which convergent studies of humans and of non-human animals have been mutually illuminating. We discuss, in turn, a path integration system for computing and updating the relationship between one's current position and other significant environmental locations, a scene recognition system guiding navigation through familiar terrain, and a reorientation system for determining one's position and heading when one has become disoriented. In each of these cases, studies of animals have provided insights into the navigation systems of humans, and studies of humans, in turn, have suggested ways to resolve longstanding controversies concerning our shared navigational mechanisms.

Path integration

Path integration is one of the primary forms of navigation found in insects, birds and mammals (Alyan & McNaughton, 1999; Collett & Collett, 2000a; Etienne, Maurer, &

former yields the current egocentric position of the nest. When multiple goals are involved, all targets can be represented as egocentric vectors relative to the animal's current position, and the movement vector is subtracted from all these vectors. Thus, the number of vectors that needs to be updated is determined by the number of individual targets the animal keeps track of (see Figure 2b). Hybrid accounts, whereby animals represent egocentric positions but allocentric environmental directions, are also possible (e.g., McNaughton, Knierim, & Wilson, 1995).

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All these accounts make equivalent predictions about the behaviour of any creature who uses path integration only to update its relationship to a single environmental location. For example, all can explain an ant's straight line homing, approach to a goal, and detours around obstacles (Bennett, 1996; Collett & Collet, 2000b). In order to distinguish between them, it is necessary to investigate path integration in a species that can update multiple locations simultaneously, where different accounts make different behavioural predictions. Humans are such a species, and so insights for distinguishing between an allocentric and an egocentric path integration system can be provided by research on human path integration (Wang & Spelke, 2000).

Timeless, allocentric spatial representations can be distinguished from dynamic egocentric spatial representations by investigating memory for a configuration of targets as the navigator moves. A fundamental property of any allocentric map, regardless of the specific frame of reference or the specific form of the encoding, is that it remains the same as the navigator moves through the environment: a house is always north of the hill whether one is in the house or on the hill. Thus, an allocentric representation should not be affected by one's changes in position or orientation. In contrast, an egocentric representation that is constantly updated according to one's movement will be affected by how such calculations are done *en route*. If there are noises in the vector summation process, so that not exactly the same vector is added to all target vectors, then the configuration of the vectors will change over time. If no enduring, allocentric representation exists, then the original configuration of vectors cannot be recovered once such deviations occur.

Based on this distinction, we developed a new paradigm to investigate whether humans navigate primarily by an allocentric cognitive map or by updating egocentric vectors (Wang & Spelke, 2000). In one study, subjects learned the locations of six objects randomly placed around the outside of a small chamber. The subjects were then placed inside the chamber, and while blindfolded, they first pointed to the objects (baseline condition). Next, they turned themselves around in the chamber until they were disoriented, and then they pointed to the targets again (disoriented condition). An allocentric cognitive map hypothesis predicts that the *relative* pointing responses to different targets should remain the same before and after disorientation, even if an absolute pointing error developed (causing all the pointing directions to rotate by the same amount). That is, a measure of the "configuration error"¹ should be as small in the disorientation condition as in the control condition. In contrast, the egocentric updating hypothesis predicts that the configuration error should increase after

¹ We measured configuration error as the standard deviation of the pointing errors to a set of targets. If subjects pointed to all targets in the same relationship to each other before and after disorientation, then they may show large errors due to their errors in determining their heading, but the error should be the same for all the targets, and thus the standard deviation should be zero, and the larger the standard deviation, the more error in the pointing configuration. For detailed discussion on assumptions and adjustments to the configuration error measure, see Wang & Spelke, 2000.

surroundings, which have the highest behavioural relevance. A consequence of this limitation is that animals should be constantly and always more disoriented relative to distal and less relevant environments, even if they are oriented to some local environment all the time and therefore are not aware of their disorientation.

These predictions were tested with undergraduate students in a windowless laboratory room at their university (Wang & Brockmole, 2003). Subjects learned the locations of five objects in the room, were blindfolded, and then were asked to point to five familiar campus buildings and to the five room targets in a random order. All subjects pointed to the room targets correctly, showing small heading errors (the mean of the errors to the individual targets, calculated as in Wang & Spelke, 2000) relative to the room. However, subjects showed large and random heading errors for the campus targets, suggesting they were completely disoriented relative to the campus (Figure 4a). Subjects did not, however, consider themselves disoriented. Human intuition fails to notice the fact that we are constantly and almost always disoriented, because disorientation relative to remote environment has few behavioural consequences. The only time we notice that we are disoriented is when we lose track of the immediate goal, which occurs infrequently.

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If humans are oriented to their immediate surroundings, then as they locomote from one environment to another they will need to engage in two additional processes. First, they need to reorient themselves to the environment they are entering. Second, they need to change the targets being updated along the way. To test these predictions, Wang & Brockmole (2003) asked subjects to walk along a path starting from the lab room, then along the hallways of the building, out through the west entrance, around the building on the streets, and finally back into the building from the north entrance. At the starting point in the lab room, subjects were asked to follow the experimenter and to stop and point to the student union as soon as they knew where it was. After they pointed to the union, they were immediately asked where the lab room was, and continued walking along the path until they were able to respond. Finally, when they had pointed to the lab room, they were shown a diagram of the room and were asked to keep walking along the path until they knew the geographical orientation of the room, and then to orient the graph in the same direction.

Most subjects had to walk outside the building before they could orient themselves relative to campus and point to the student union. Moreover, by the time they were oriented to campus, they had lost track of the room they had departed from; most people had to continue walking further along the path towards the north entrance before they could point to the room. Interestingly, even after they were able to point to the room, most subjects had to walk further along and back into the building before they knew the room's orientation (Figure 4b). Thus, subjects clearly showed alterations of their sense of direction relative to different environments.

There are two possible reasons that the subjects had to walk a certain distance to respond to the targets. First, the subjects may have needed to walk because they reoriented themselves to the upcoming environment at given spatial locations according to certain cues. Alternatively, they may have walked further because they needed a certain amount of time to compute the direction of the targets. For example, according to a nested cognitive map model (e.g., Hirtle & Jonides, 1985; Huttenlocher, Hedges, & Duncan, 1991; McNamara, 1986; Stevens & Coupe, 1978; Taylor & Tversky, 1992), subjects may know where they are relative to the room, where the room is relative to the building, and where the building is relative to other buildings on campus. In order to point to the student union, subjects would need to combine these spatial representations and compute the direction of the union relative to themselves in

with their body orientation aligned in roughly the same horizontal direction (Collett & Rees, 1997). As a result, the image of the feeder on the retina was roughly the same each time an individual insect approached it. Careful analysis of the motion patterns of the wasps during their first departure from a newly discovered feeder revealed that they flew in arcs roughly centred on the feeder and turned to face the feeder towards the end of each arc, at inspection points that were precisely arranged along lines extending out from the feeder (Collett & Lehrer, 1993). The findings suggest that insects acquire "snapshots" of relevant locations and recognize them by image matching. However, it is possible that insects process these images further, for example to reconstruct some depth information in the scene.

Some data suggest that bees and wasps can capture 3D depth information in their place recognition system. Lehrer & Collett (1994) tested the landmark learning of honeybees as they approached and departed from a feeder and found that bees focused on different aspects of a landmark in these two cases. When trained to forage at a feeder near a cylinder landmark that was revealed only during arrival, bees learned the apparent landmark size but not distance; when trained with a landmark revealed only during departure, bees learned its absolute distance. Since bees usually "turn back and look" during the first few departures from a new feeder (Collett & Lehrer, 1993), the authors argued that this 3D structure of the environment is important during initial learning to "identify those landmarks close to a foraging site which will specify accurately the site's position." The dominant strategy later on is by view matching. In either case, honey bees and wasps seem to obtain an egocentric representation of the target environment. Moreover, wood ants can store multiple snapshots of a familiar beacon from different vantage points, so that a significant place can be recognized from multiple angles (Judd & Collett, 1998).

Mammals form similar representations of scenes. For example, hamsters show selective exploration of moved objects in their environment, but their detection of moved objects is impaired when they enter the environment from a novel vantage point (Thinus-Blanc, Durup & Poucet, 1992), and detection fails altogether if they are introduced to the environment from a different direction on each visit, suggesting they stored local views of the environment. Similarly rats trained to escape to an invisible platform in a water maze show impaired localization of the maze if they are released into a portion of the maze that they never explored, suggesting that they use view-specific representations to recognize its location (Sutherland, Chew, Baker, & Lingard, 1987).

The use of view-dependent representations appears to be constrained by the animal's path integration system. For example, ants generally rely on vector-based information when landmark-based and vector-based information conflict (Wehner & Menzel, 1990; Wehner, Michel & Antonsen, 1996). Similarly, bees tend to reject landmark information when the landmarks are rotated and therefore contradict the sense of position and orientation specified by the path integration system (e.g., Cartwright & Collett, 1982; Collett & Cartwright, 1983). Other studies suggest that ants and bees sometimes rely on the view-dependent place recognition system rather than on path integration when they travel through familiar terrain (Collett & Collett, 2000a). When they approach an unfamiliar area or detect new landmarks, however, path integration comes to dominate (Collett et al, 1999). Similar combinations of path integration with view-based information have been shown in rodents (Griffin, & Etienne, 1998; Georgakopoulos, & Etienne, 1997).

Like insects and other mammals, humans use view-dependent representations to recognize objects and scenes (Bülthoff, Edelman, & Tarr, 1995; Diwadkar & McNamara, 1998; Edelman & Bülthoff, 1992; Humphrey & Khan, 1992; Logothetis & Pauls, 1995; Shepard & Cooper, 1982; Shepard & Metzler, 1971; Tarr, Williams, Hayward, & Gauthier, 1998; Tarr & Pinker, 1989; Ullman, 1989). For example, Tarr & Pinker (1989) trained subjects with a set of novel objects presented at a specific vantage point (i.e., a specific "view"). During testing,

Studies of place recognition provide a second example in which research on a wide range of non-human animals has converged with research on humans, and in which the two research traditions have been mutually illuminating. Studies of insects, rodents, and humans provide compelling information that the primary long-term representations of places in the layout are viewpoint-specific. Studies of insects first suggested that these place representations serve to specify the initial direction of the next leg of a complex journey (Collett & Collett, 2000a): a suggestion confirmed by studies of humans navigating in virtual environments (Gillner & Mallot, 1998). Studies of humans further suggest that scenes are dynamically updated over motion, so that long-term memory representations encoded as single views do not provide the strongest or most accurate representations when the navigator moves to a new vantage point (Simons & Wang, 1998; Wang & Simons, 1999). It will be interesting to see whether the same updating effects occur in other animals.

Reorientation

In many animals, the path integration system and the view-dependent scene recognition system are complemented by a reorientation system, which restores the representation of the spatial relationship between the animal and its environment when path integration is fully disrupted. The mechanisms of reorientation have been studied most extensively in rodents (Cheng, 1986; Gallistel, 1990; Margules & Gallistel, 1988). Hungry rats explored a rectangular chamber where they were allowed to find but not to consume food that was partially buried. Then rats were removed from the chamber, disoriented by repeated turning in a closed box, and returned to the chamber where they were allowed to search for the food, now fully buried. In these experiments, multiple visual and olfactory landmarks marked the food's location: for example, the food might be buried next to a corner with a distinctive odour of anise and a distinctive striped pattern of lighting. Rats, however, ignored these landmarks and searched for the food at two locations that were marked by different landmarks but were equivalent with respect to the geometry of the chamber: the correct location and the symmetrical location on the opposite side of the room (Figure 7a). Based on this performance, Cheng and Gallistel (1984) proposed that rats reorient by virtue of a "geometric module": an encapsulated system that operates only on a geometric description of the environment. They noted, however, that their terminology was somewhat misleading. The locations of layout features such as a pattern of striped lights can, in principle, be described geometrically, and yet rats failed to reorient by these features. Cheng's findings suggest that rats reorient in accord with the shape of the extended surface layout, and not in accord with the shapes, brightness, or odors of other entities in the environment.

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Inspired by this line of research, Hermer-Vazquez tested for a modular reorientation process in humans by presenting 1.5- to 2-year-old children with a variant of Cheng's navigation task (Hermer & Spelke, 1996). Children first watched as a favored toy was hidden in one of four corners of a rectangular chamber, then were lifted and turned repeatedly with eyes closed to induce a state of disorientation, and finally were released and encouraged to find the toy. In different experiments, the location of the toy was specified by the distinctive color of a single wall (e.g., the toy might be in the only corner having a blue wall on the left and a white wall on the right) or by the presence of a distinctive landmark object (e.g., the toy might be in the corner to the left of a toy with which the child had been playing). Like rats, children searched reliably and equally both at the correct corner and at the geometrically equivalent opposite location (Figure 7b). Children's successful use of room geometry showed that they were

used for a different purpose, and in which use of that information would improve reorientation performance? An experiment by Wang et al. (1999) provides such a case. Children were observed over multiple sessions in a square room with one bright red wall. Over the course of these sessions, children learned that they could produce an interesting event (a musical sequence played outside the room) by tapping on the red wall. Then children were disoriented and were encouraged either to make the music or to locate an object hidden to the left or right of the red wall. When encouraged to make the music, children immediately turned to the red wall and hit it. When encouraged to find the object, the same children searched at random in the four corners, ignoring the red wall when disoriented (and searching correctly when oriented) (Figure 8c). These findings indicate that children noticed and remembered the red wall and were able to use it as a direct cue to an action. In contrast, children failed to use the red wall to reorient themselves and so failed, on most trials, to locate the desired object (see also Hermer & Spelke, 1996, and Gouteux & Spelke, 2001, for further evidence for encapsulation of the reorientation system).

Despite these findings, research on a variety of animals provides evidence that disoriented organisms respond to non-geometric landmarks under certain conditions, challenging the evidence for an encapsulated geometric system. First, both rats and monkeys who have been given extensive training have learned to respond to non-geometric information when disoriented (Cheng, 1986; Gouteux, Thinus-Blanc, & Vauclair, 2000). Second, untrained rats and fish have been shown to respond reliably to non-geometric information when they are tested in a highly motivating escape task, rather than a less-motivating foraging task (Dudchenko et al., 1997a; Sovrano et al., 2002). Third, minimally trained children have been shown to search in the correct relation to a distinctive landmark if the landmark enclosed the hidden object (Gouteux & Spelke, 2001), and they have shown a small but discernible tendency to use the landmark when it served as a distinctive background for the object (Stedron, Munakata & O'Reilly, 2000).

There are two ways to interpret these findings: either animals and children reorient by means of an unencapsulated mechanism that is sensitive to a wide range of information, or they reorient by means of a modular system, and their responses to non-geometric information are the products of other systems. Cheng (1986) and Gallistel (1990) favour the latter view, and suggest that for trained animals (and, by extension, animals tested in highly motivating tasks), the geometric reorientation system is enhanced by the scene matching system described in the last section. Recent studies with young children provide empirical tests of their conjecture and shed further light on the mechanisms of navigation.

Evidence that view-specific representations enhance children's spatial performance, but fail to penetrate the reorientation system, comes from an experiment by Gouteux et al (2001), in which disoriented children searched for an object hidden in one of three containers. Although children failed to find the object when the containers were indistinguishable, they reliably retrieved it when the hiding container differed from the other containers in colour and shape, providing evidence that disoriented children were able to use non-geometric information (the container's distinctive properties) to guide their search. To investigate whether children reoriented by this information, a further experiment was conducted in which two of the three containers had the same shapes and colours and the third was distinctive, and in which the object was hidden successively in each of the three containers. If the container with a unique colour and shape served as a cue to reorientation, then children should have searched with equal success regardless of where the object was hidden. In fact, however, children searched correctly when the object was hidden in the single distinctive container, and they searched equally at the other two containers when the object was hidden in one of them (Gouteux & Spelke, unpublished). These findings provide evidence that children form local, view-specific representations of significant locations, and they can use these representations to find a hidden

show heightened firing when the animal moves through a particular location of the environment ("place cells": O'Keefe & Nadel, 1978; McNaughton, Knierim, & Wilson, 1995; Taube, 1995), and some cells in surrounding cortical areas show heightened firing when the animal faces in a particular direction ("head direction cells": Taube, Muller, & Ranck, 1990a, b). Interestingly, place cells appear to be particularly responsive to the geometry of the enclosure, for their firing fields are highly dependent on the distance of the animal from a set of walls (O'Keefe & Burgess, 1996). Moreover, place fields are tuned with experience to fire differentially in environments of different shapes, and they generalize their firing patterns to new environments with the same shape but markedly different non-geometric properties (Lever, Wills, Cacucci, Burgess & O'Keefe, 2002; Lever et al., this volume). These findings accord with the behavioural evidence that the geometry of the surrounding layout plays a privileged role in animal navigation.

Further findings nevertheless raise questions about the existence of a geometric module for reorientation. When rats are observed in a simple enclosure (typically, a circular chamber) with a simple non-geometric landmark (typically, a segment of the circular walls presented at a distinctive brightness), the firing fields of place cells and firing directions of head-direction cells tend to rotate with rotations of the landmark. After extensive familiarisation in the chamber while the animal was oriented and the non-geometric landmark occupied a stable location, moreover, place and head-direction cells aligned their firing fields in accord with the location of the non-geometric landmark when the animal was disoriented and the landmark was rotated (Knierim et al., 1995; although see Dudchenko et al., 1997b). If these cells signal the animal's location on an allocentric map, then these findings would imply that rats reorient by non-geometric information in an environment that is both highly familiar and that has a less informative shape than the rectangular environments favoured by behavioural studies of reorientation.

Accordingly, studies with children have tested whether the reorientation system is sensitive to non-geometric information in geometrically simple environments: a room that was either square or circular and that contained one sector of distinctive colour and brightness (Wang, et al., 1999; Gouteux & Spelke, 2001). Children failed to reorient by the red panel in either environment, providing no evidence that they reorient by non-geometric information when the geometry of the layout is less informative. Further studies with children tested whether the reorientation system uses non-geometric information in familiar environments, by allowing children to become familiar with the test chamber over a series of sessions before testing their reorientation (Wang et al., 1999). Even after extensive familiarization with the chamber, children failed to reorient by the non-geometric landmark. If these results with children can be generalized to rats, they suggest that the firing patterns of place and head-direction cells do not reflect the activation of a cognitive map or a process of reorientation. What, then are the cells coding for?

The research reviewed above suggests one possibility. Because the cylindrical environments in which rats foraged were fairly large, the non-geometric landmark may have served as a directional signal rather than as a positional cue, as in the experiments by Dibble et al. (2003). To test this and other possibilities, it is essential to record place and head-direction cell activity while animals are performing the reorientation task. Although behavioural and neurophysiological recording studies have been conducted in the same environments (e.g., Dudchenko et al., 1997a, 1997b), neurophysiological studies have not, to our knowledge, recorded from cells while animals performed a reorientation task. Such recordings are necessary for understanding the neural mechanisms of reorientation.

In summary, the finding that disoriented animals and children sometimes search for objects in accord with non-geometric features of the environment does not imply that they reorient by these features. There are at least two possible mechanisms that can allow an animal with a

Although the rhythm shadowing task led to an overall degradation of performance, subjects continued to locate the object both in accord with the shape of the room and in accord with the blue wall. In contrast, the verbal shadowing task abolished subjects' ability to locate the object in relation to the blue wall while largely sparing their ability to locate the object in relation to the shape of the room. These findings provide evidence that the encapsulated reorientation system found in rats and in human children is present and functional in adults. Under normal conditions, however, this navigation system is supplemented by a different system of representation that depends in some way on human language.

Studies of reorientation provide our third and last example of the mutually illuminating effects of research on navigation in animals and humans. Experiments with rats first suggested the hypothesis of a geometric module. Studies of children then confirmed that the reorientation system has the three signature limits of modular systems: domain-specificity, task-specificity, and encapsulation. Further studies of animals and children then focused on the interplay of this system with other systems, particularly the scene recognition system and a system for determining one's heading from directional information: an interplay that enables disoriented animals and humans to benefit from non-geometric information, despite the limits on their reorientation system. Finally, research on human adults has begun to suggest why human navigation appears, intuitively, to be so different from navigation in animals. Whereas the basic mechanisms of navigation are task-specific and encapsulated and give rise to multiple, fragmentary representations of the environment, specifically human systems of representation such as spatial maps and natural language are general purpose systems that re-represent this information (Karmiloff-Smith, 1992) within a single, unitary format. These uniquely human, constructed representations may be most accessible to human intuition. The basic spatial representations on which they build, however, are the multiple, encapsulated mechanisms of path integration, scene recognition, and reorientation that humans share with other animals.

Conclusions

Much has been learned about human navigation from the study of other animals. For example, humans can navigate by path integration as do ants, returning to the origin of a path after blindfolded walk. Moreover, humans possess a view-dependent scene recognition system similar to that found in bees and rodents. When people are fully disoriented, they reorient themselves by analysing the shape of the surrounding layout and computing the congruence of that shape to the remembered shape of the layout before disorientation, as do birds and rodents. All these findings suggest that the basic representations by which people navigate are very different from the unitary, permanent, allocentric maps of geographers.

Studies of human navigation can also provide insights into the navigation mechanisms of other animals. For example, studies of humans suggest that path integration is a process of forming, maintaining, and dynamically updating an egocentric representation of significant environmental locations, rather than updating a vector of the animal's allocentric position in a cognitive map. Studies of scene recognition suggest that multiple, local representations serve to capture information about a scene, and that static, enduring scene representations are either weaker or less precise than dynamically updated representations of objects. Studies of reorientation suggest that reorientation depends on a modular system that operates on a purely geometric representation of extended surfaces, and that the performance of disoriented animals is enriched by mechanisms for determining compass heading from distant cues and by the processes of view-dependent scene recognition just described. All this research

References

- Alyan, S., & McNaughton, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience*, 113, 19-31.
- Bennett, A. T. D. (1996). Do animals have cognitive maps? *J. Exp. Biol.* 199, 219-224.
- Berthoz, A., Israel, I., Francois, P. G., Grasso, R. & Tsuzuku, T. (1995). Spatial memory of body linear displacement: What is being stored? *Science*, 269, 95-98.
- Biegler, R. & Morris, R. G. M. (1996). Landmark stability: Studies exploring whether the perceived stability of the environment influences spatial representation. *Journal of Experimental Biology*, 199, 187-193.
- Bülthoff, H. H. & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the United States of America*, 89, 60-64.
- Bülthoff, H. H., Edelman, S., & Tarr, M. J. (1995). How are three-dimensional objects represented in the brain? *Cerebral Cortex*, 3, 247-260.
- Cartwright, B. A & Collett, T. S. (1982). How honey bees use landmarks to guide their return to a food source. *Nature*, 295, 560-564.
- Cartwright, B. A & Collett, T. S. (1983). Landmark learning in bees: Experiments and models. *Journal of Comparative Physiology*, 151, 521-543.
- Cheng, K. & Gallistel, C. R. (1984). Testing the geometric power of an animal's spatial representation. In H. L. Roitblat, T. G. Bever, and H. S. Terrace (Eds.), *Animal Cognition* (p. 409-423). Hillsdale, NJ: Erlbaum.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23, 149-178.
- Cheng, K., Collett, T. S., Pickhard, A., & Wehner, R. (1987). The use of visual landmarks by honey bees: bees weight landmarks according to their distance from the goal. *Journal of Comparative Physiology*, 161, 469-475.
- Collett, M. & Collett, T. S. (2000a). How do insects use path integration for their navigation? *Biological Cybernetics*, 83, 245-259.
- Collett, M., Collett, T. S., & Wehner, R. (1999). Calibration of vector navigation in desert ants. *Current Biology*, 9, 1031-1034.
- Collett, T. S. & Cartwright, B. A. (1983). Eidetic images in insects: Their role in navigation. *Trends in Neuroscience*, 6, 101-105.
- Collett, T. S. & Collett, M. (2000b). Path integration in insects. *Current Opinion in Neurobiology*, 10, 757-762.
- Collett, T. S. & Lehrer, M. (1993). Looking and learning a spatial pattern in the orientation flight of the wasp *vespula-vulgaris*. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 252, 129-134.
- Collett, T. S. & Rees, J. A. (1997). View-based navigation in Hymenoptera: Multiple strategies of landmark guidance in the approach to a feeder. *Journal of Comparative Physiology A-Sensory Neural & Behavioral Physiology*, 181, 47-58.

- Hermer-Vazquez, L., Moffet, A. & Munkholm, A. (2001). Language, space, and the development of cognitive flexibility in humans: The case of two spatial memory tasks. *Cognition*, 79, 263-299.
- Hermer-Vazquez, L., Spelke, E. S., & Katsnelson, A. (1999). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology*, 39, 3-36.
- Hirtle, S. C., & Jonides, J. (1985). Evidence of hierarchies in cognitive maps. *Memory & Cognition*, 13, 208-217.
- Humphrey, G. K., & Khan, S. C. (1992). Recognizing novel views of three-dimensional objects. *Canadian Journal of Psychology*, 46, 170-190.
- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, 98, 352-376.
- Judd, S. P. D. & Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature*, 392, 710-714.
- Karmiloff-Smith, A. (1992). Beyond modularity: A developmental perspective on cognitive science. Cambridge MA: MIT Press.
- Knierim, J. J., Kudrimoti, H. S. & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. *Journal of Neuroscience*, 15, 1648-1659.
- Landau, B., Spelke, E. S., & Gleitman, H. (1984). Spatial knowledge in a young blind child. *Cognition*, 16, 225-260.
- Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddlers' use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology*, 80, 225-244.
- Learmonth, A. E., Nadel, L. & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science*, 13, 337-341.
- Lehrer, M., & Collett, T. S. (1994). Approaching and departing bees learn different cues to the distance of a landmark. *Journal of Comparative Physiology A-Sensory Neural & Behavioral Physiology*, 175, 171-177.
- Lever, C., Wills, T., Cacucci, F., Burgess, N. & O'Keefe, J. (2002). Long-term plasticity in hippocampal place cell representation of environmental geometry. *Nature*, 416, 90-94.
- Logothetis, N. K., & Pauls, J. (1995). Psychophysical and physiological evidence for viewer-centered object representations in the primate. *Cerebral Cortex*, 3, 270-288.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, 122, 73-91.
- Mallot, H. A. & Gillner, S. (2000). Route navigating without place recognition: What is recognised in recognition-triggered responses? *Perception*, 29, 43-55.
- Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning & Behavior*, 16, 404-410.
- McNamara, T. P. (1986). Mental representations of spatial relations. *Cognitive Psychology*, 18, 87-121.
- McNaughton, B. L., Knierim, J. J. & Wilson, M. A. (1995). Vector encoding and the vestibular foundations of spatial cognition: neurophysiological and computational

- Sutherland, R. J., Chew, G. L., Baker, J. C., & Linggard, R. C. (1987). Some limitations on the use of distal cues in place navigation by rats. *Psychobiology*, 15, 48-57.
- Tarr, M. J. (1995). Rotating objects to recognize them: A case study on the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review*, 2, 55-82.
- Tarr, M. J., & Pinker, S. (1989). Mental rotation and orientation-dependence in shape recognition. *Cog. Psych.*, 21, 233-282.
- Tarr, M. J., Bülthoff, H. H., Zabinski, M. & Blanz, V. (1997) To what extent do unique parts influence recognition across changes in viewpoint? *Psychological Science*, 8, 282-289.
- Tarr, M. J., Williams, P., Hayward, W. G., & Gauthier, I. (1998). Three-dimensional object recognition is viewpoint-dependent. *Nature Neuroscience*, 1, 275-277.
- Taube, J. S. (1995). Place cells recorded in the parasubiculum of freely moving rats. *Hippocampus*, 5, 569-583.
- Taube, J. S., Muller, R. U. & Ranck, J. B. (1990a). Head-direction cells recorded from the postsubiculum in freely moving rats: I. Description and quantitative analysis. *The Journal of Neuroscience*, 10, 420-435.
- Taube, J. S., Muller, R. U. & Ranck, J. B. (1990b). Head-direction cells recorded from the postsubiculum in freely moving rats: II. Effects of environmental manipulations. *The Journal of Neuroscience*, 10, 436-447.
- Taylor, H. A., & Tversky, B. (1992). Descriptions and depictions of environments. *Memory & Cognition*, 20, 483-496.
- Ullman, S. (1989). Aligning pictorial descriptions: An approach to object recognition. *Cognition*, 32, 193-254.
- Wang, R. F., & Brockmole, J. R. (2003). Human navigation in nested environments. *Journal of Experimental Psychology: Learning, Memory & Cognition*, 29, 398-404.
- Wang, R. F., & Simons, D. J. (1999). Active and passive scene recognition across views. *Cognition*, 70, 191-210.
- Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, 77, 215-250.
- Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by human children: a comparison with rats. *Behavioral Neuroscience*, 113, 475-485.
- Warren, D. H., Scott, T. E. (1993). Map alignment in traveling multisegment routes. *Environment & Behavior*, 25, 643-666.
- Wehner, R. & Wehner, S. (1990). Insect navigation: Use of maps or Ariadne's thread? *Ethology, Ecology and Evolution*, 2, 27-48.
- Wehner, R. & Srinivasan, M. V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology*, 142, 315-318.
- Wehner, R., & Lanfranconi, B. (1981). What do the ants know about the rotation of the sky? *Nature*, 293, 731-733.
- Wehner, R. & Menzel, R. (1990). Do insects have cognitive maps? *Annual Review Of Neuroscience*, 13, 403-414.

Figure Legends

Figure 1. Path integration by (a) desert ants (after Wehner & Srinivasan, 1981) and (b) humans (after Loomis et al, 1993). Panel a shows an ant's homeward trajectory after it was passively transported to a testing ground and released at S. N* indicates where the nest would be if the ant followed the same homing vector. Panel b shows the returning paths of a blindfolded human adult after walking along a two-leg path without vision. The dotted lines indicate the outward path, the dots (S) indicate the end positions, and the cross (N*) indicates the starting position (i.e., the "home").

Figure 2. Contrasting models of path integration by (a) updating of the navigator's allocentric position on a cognitive map, and (b) updating of the egocentric positions of significant locations. In panel a, target positions (e.g., the Feeder) are represented by vectors relative to home. The animal represents its position relative to home as a vector H , and when it moves, it adds the movement vector M to H to compute its new position relative to home (H'). In panel b, all targets are represented as egocentric vectors. As the animal moves, it subtracts the movement vector M from these vectors (A & B) individually to compute the new egocentric vectors (A' & B').

Figure 3. Human subjects' accuracy at representing a configuration of objects before and after disorientation (after Wang & Spelke, 2000). Panel a shows the apparatus. Six target objects surrounded the testing chamber and four lights (solid circles) illuminated the chamber and served as directional cues when only one light was on. Panel b shows the configuration errors before (baseline) and after (test) the turning, in the disorientation, oriented turning, and reorientation conditions. Configuration errors increased in the disorientation and reorientation conditions, but not in the oriented turning condition. These results suggest that subjects' accurate spatial representation depends on their estimation of self-position/orientation, thus supporting the egocentric updating model.

Figure 4. Human subjects' path integration in nested environments. Panel a shows the heading errors for the room and campus. Subjects were oriented relative to the room while at the same time disoriented relative to campus. Panel b shows the positions at which human subjects become oriented to various targets while walking along a path, which started from an interior room, continued along the hallways and exited the building at the lower right corner (west entrance), and then continued around the building and re-entered the building at the upper left corner (north entrance). (after Wang & Brockmole, 2003).

Figure 5. View-dependent scene recognition by (a) bees foraging for nectar with one landmark (left) and multiple landmarks (right) after the size and distance between the landmarks changed (after Cartwright & Collett, 1983). The bees searched a position that preserved the visual angle of either a single landmark, or the relative position of two landmarks. (b) Humans navigating through a virtual environment after the landmarks changed. The filled triangle indicates the behavioural choice each landmark was associated with during training. Control: no landmark change. Within place: exchange of peripheral landmarks within place. Consistent: exchange of landmarks across places but the behavioural choices associated with the landmarks are consistent with the correct response. Inconsistent: exchange of landmarks across places and the behavioural choices associated with the landmarks are inconsistent with the correct response. The numbers indicate the percentage of correct behavioural choices. (after Mallot & Gillner, 2000).

Figure 6. Human subjects' accuracy at detecting a displaced object when tested at the original or at a different viewing position (after Wang & Simons, 1999). Panel a shows the

a

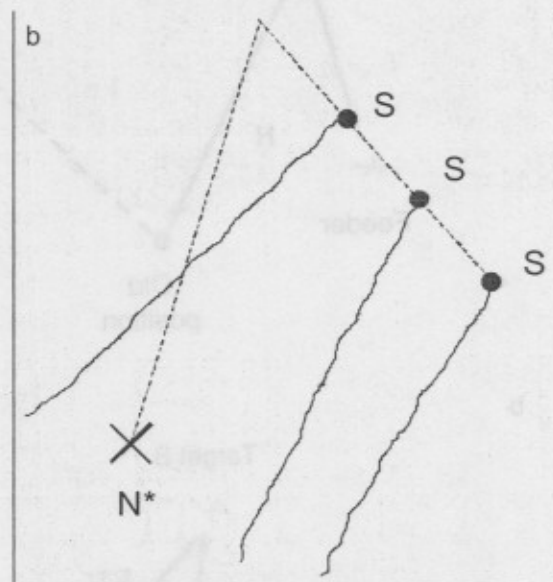
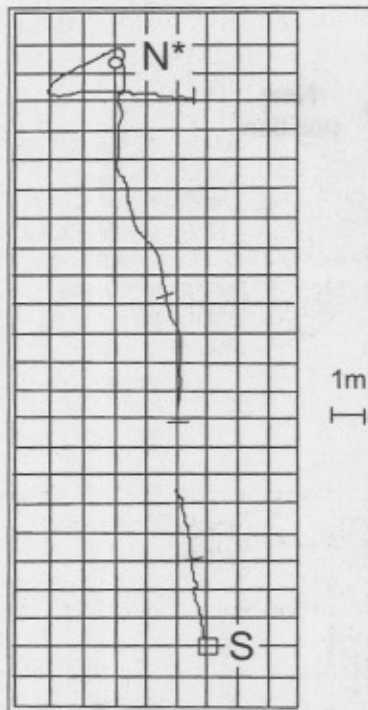


Figure 1

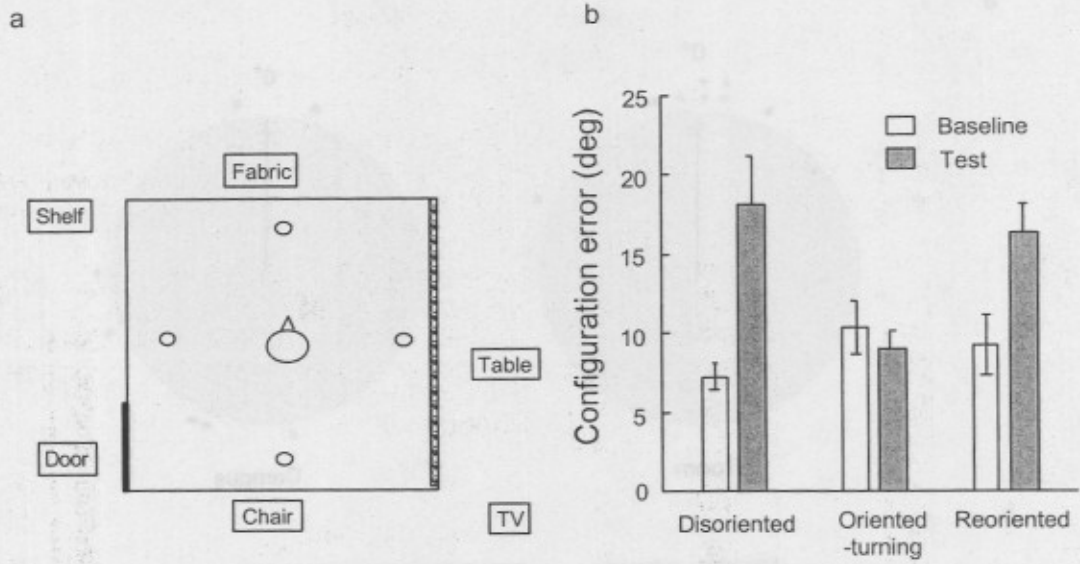


Figure 3

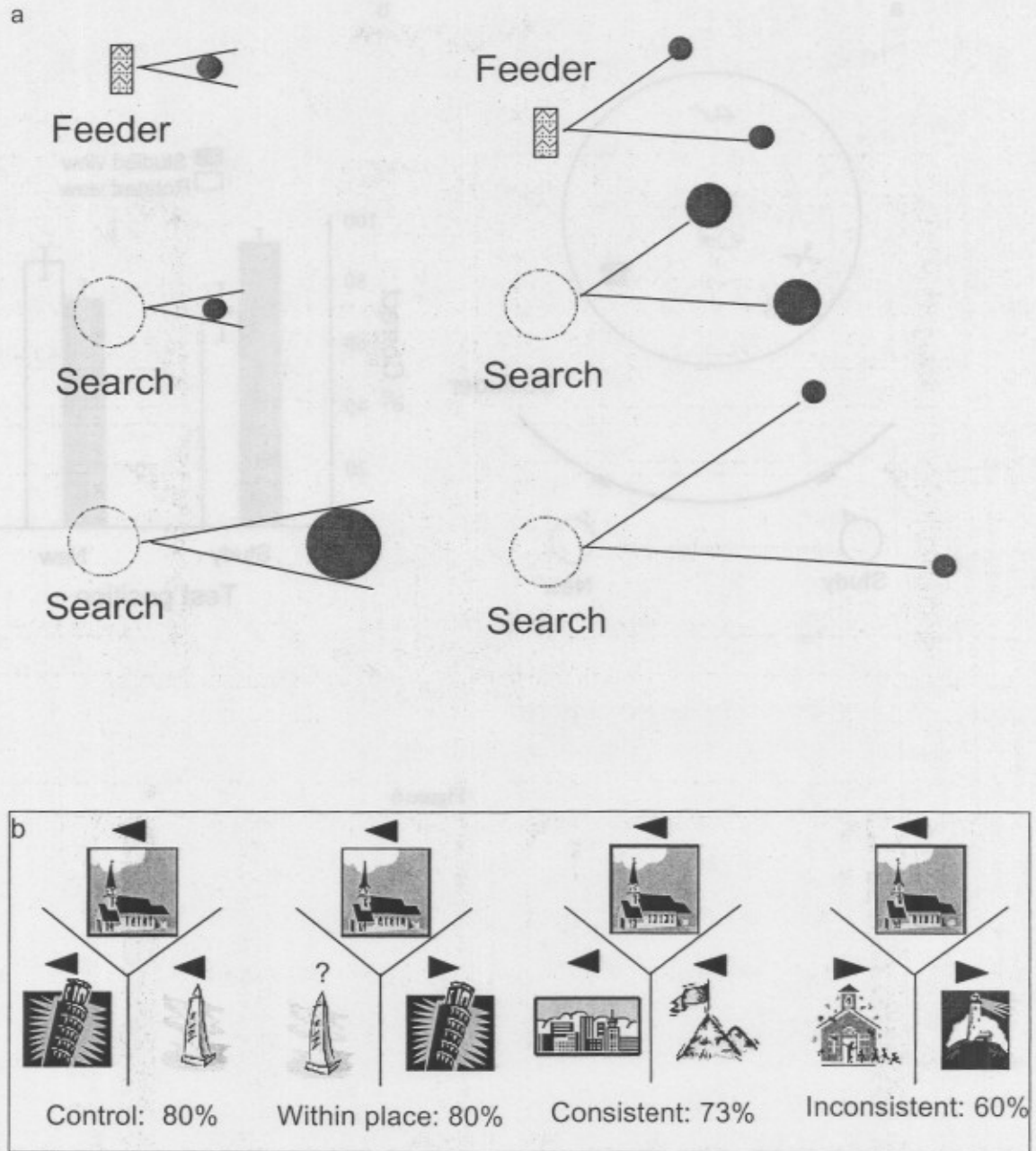


Figure 5

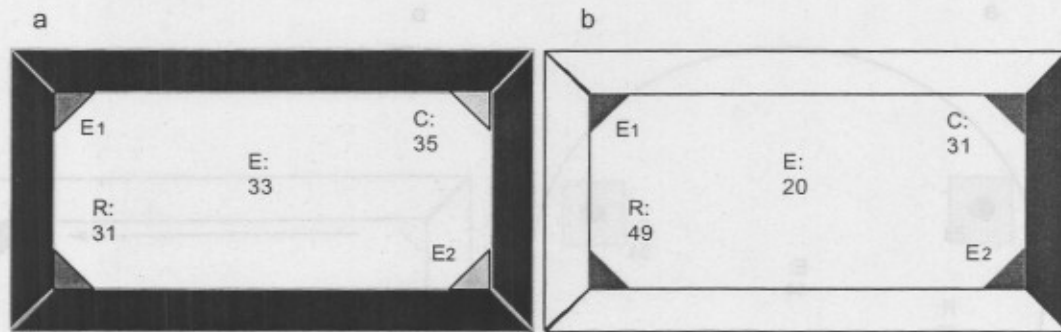
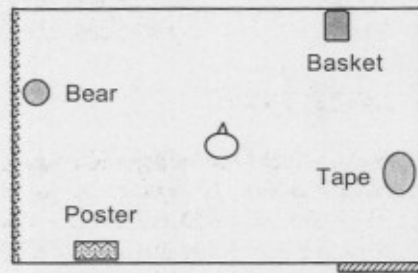


Figure 7

a



b

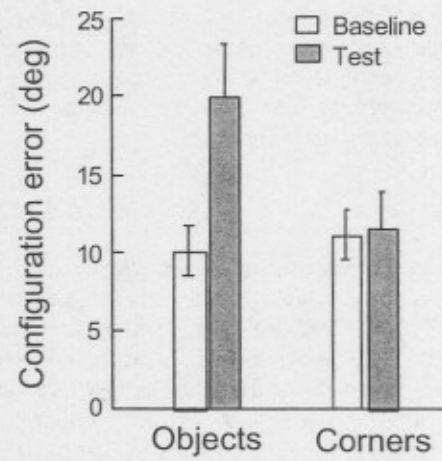


Figure 9