

Human spatial representation: insights from animals

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Human navigation is special: we use geographic maps to capture a world far beyond our unaided locomotion. In consequence, human navigation is widely thought to depend on internalized versions of these maps—enduring, geocentric ‘cognitive maps’ capturing diverse information about the environment. Contrary to this view, we argue that human navigation is best studied in relation to research on navigating animals as humble as ants. This research provides evidence that animals, including humans, navigate primarily by representations that are momentary rather than enduring, egocentric rather than geocentric, and limited in the environmental information that they capture. Uniquely human forms of navigation build on these representations.

Since the work of Tolman [1], many psychologists have argued that mammalian navigation depends on internal representations that are *enduring*, *geocentric*, and *comprehensive*: ‘cognitive maps’ of the environment. Suggestive evidence for cognitive maps came from studies of rodents, who systematically explore novel environments, detect displaced landmarks, and take new paths between familiar locations [1–3]. More recently, however, much of the mammalian spatial behavior that was attributed to cognitive maps has been found to depend on representations of quite a different sort: representations that are *dynamic*, *egocentric*, and *limited* to a restricted subset of environmental information. Here we review briefly research on navigating animals from ants to primates and then turn to research on human navigation. We suggest that momentary, egocentric, and limited representations underlie much of human spatial behavior, including aspects of human navigation that have been taken as paradigmatic evidence for cognitive maps.

We focus on three systems that underlie navigation in diverse animals: (1) a path integration system that operates by dynamic updating, (2) a place recognition system that operates by template matching of viewpoint-dependent representations of landmarks, and (3) a reorientation system that operates by congruence-finding on representations of the shape of the surface layout. After reviewing the evidence for these systems from studies of animal navigation, we consider evidence for these systems from studies of humans. Finally, we ask what might account for the special character of human navigation.

Navigation systems in animals

Path integration

Path integration is a process by which the relation of the animal to one or more significant places in the environment is updated continuously as the animal moves. For example, the position of the nest relative to a foraging animal changes as the animal moves through the environment. By representing the nest’s egocentric position as a vector, specifying both the radial direction and the distance of the nest from the animal’s current position and heading, and by continuously subtracting from it a second vector specifying the direction and distance traveled from the last moment of updating to the current one, the resulting vector corresponds to the current egocentric position of the home. (Alternatively, the nest could be represented as the origin of a geocentric coordinate system, the ant’s current position represented as a vector specifying its distance and direction from the nest, and updating could occur by vector addition. With one fixed and one changing position, these two representational schemes are equivalent.)

Path integration has been found to be one of the primary forms of navigation in insects [4–6], birds [7,8], and mammals [9–13]. For example, desert ants forage by traveling on new and apparently random routes and then return home on a direct path once food is found. If a homeward-bound ant is passively carried in darkness to a new location, it moves on a parallel path for the appropriate distance [14] (Fig. 1). This finding indicates that ants do not find their way home by detecting any perceptible features of the environment, for such features either are not available or conflict with the chosen direction when ants are displaced into new territory. Instead, ants rely on a global compass system (primarily provided by the sun), measure the horizontal distance they travel (correcting for vertical displacements [15]), and update their relation to the nest throughout their movement.

Although path integration allows for sophisticated navigation performance, including navigation around obstacles [16] and towards food sources [17], it shows two characteristic limitations. First, it is subject to cumulative errors and therefore must be corrected or reset to provide accurate guidance for navigation. Second, path integration is a dynamic system for keeping track of the home vector continuously and therefore is subject to forgetting. When homeward-bound ants are placed in a jar and allowed to continue their journey after a variable delay, their ability to follow the appropriate vector course vanishes after a few days [18]. To overcome these limits, path integration is complemented by other, more enduring spatial representations.

View-dependent place recognition

The primary form of place recognition in insects has been characterized as a ‘snapshot’ view-matching system [19–23]. Evidence for snapshot representations comes from experiments in which bees are trained

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to forage at a place specified by landmarks and then the food sources and landmarks are moved or altered: the bees tend to search where landmarks subtend the same visual angles as during training. Both wasps

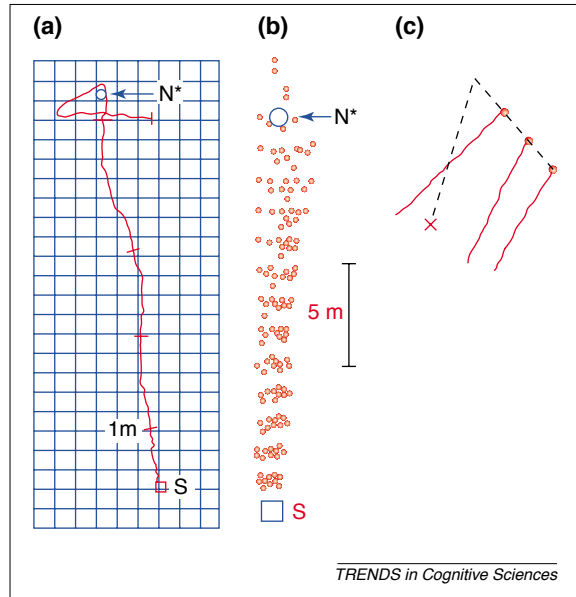


Fig. 1. The path integration system in ants and humans. (a) The homing trajectory of an ant transported from the feeder, from the releasing point (S) to the location where the nest would have been had the ant not been transported (N*). (b) The superimposed homing trajectory of 10 ants. Each dot represents the position of one ant recorded at 10-s intervals during the return journey (redrawn from Fig. 2, Ref. [14]). (c) The paths of a representative blindfolded human subject returning to the starting point of two-leg paths of variable length (redrawn from Fig. 5, Ref. [34]). The blindfolded subject was led along the paths (indicated by the dashed line) and asked to return to the starting point at the end of the second leg (indicated by the dot) (corresponding to the ant's release point). The cross indicates the starting point of the locomotion (corresponding to the nest).

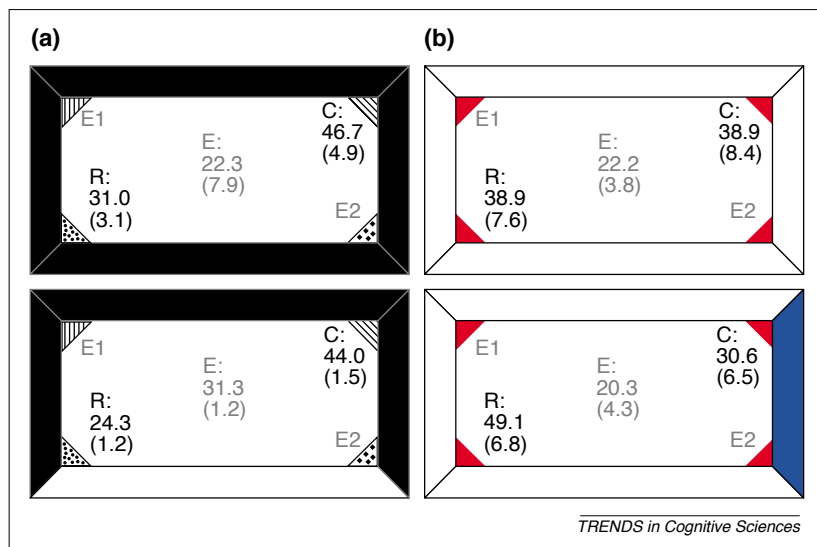


Fig. 2. The reorientation system in rats and children. (a) The search pattern of disoriented rats in a rectangular box with distinctive visual and olfactory markings at each corner (redrawn from Table 1, Ref. [30]). The box had either four black walls (upper panel) or one white wall and three black walls (lower panel). (b) The search pattern of disoriented children in a rectangular chamber with either four white walls (upper panel) or one blue wall and three white walls (lower panel) (redrawn from Fig. 4, Ref. [55]). Each figure presents the percentage of search trials (with standard errors) at the correct location (C), the rotationally equivalent location (R), and elsewhere (E, in gray), which includes the two geometrically incorrect corners (E1 and E2). The search pattern was not affected by a non-geometric cue for either rats or children.

and honeybees acquire these view-dependent representations by approaching the feeder from a constant direction, with their body orientation aligned in roughly the same horizontal direction, so that the visual image of the scene is roughly the same each time an individual insect approaches the feeder [21,22], whereas wood ants store multiple snapshots of a familiar landmark from different vantage points so as to recognize it from multiple angles [23]. Under certain conditions, place representations capture information about the distances and the directions of landmarks [24]. View-dependent place representations with richer depth information guide navigation in mammals and in insects. For example, rats tested in a water maze tend to approach a hidden platform from a familiar direction, suggesting that they use view-specific representations to recognize their location [25].

In familiar terrain, ants and bees use view-dependent place representations to navigate from one location to another [20]. When an ant's scene representations are placed into conflict with path integration, place representations typically have a greater influence on the ant's initial path, and path integration comes to dominate later in the journey if no new landmarks are detected [26]. These findings suggest that ants use path integration to specify the global direction and distance of the nest, both in familiar and in novel territory, and use view-dependent place representations to specify local regions of a journey through familiar territory.

Reorientation

In vertebrates, the path integration system is further complemented by a reorientation system that restores the spatial relationship between the animal and its environment when path integration is fully disrupted. Reorientation has now been studied in a variety of animals including primates [27], birds [28], fish [29], and especially rodents [13,30,31]. Cheng [30] allowed hungry rats to view the location of food in a rectangular chamber with multiple visual and olfactory landmarks, and then disoriented the rats and observed their subsequent search. Rats ignored the landmarks and searched for the food both at the correct location and at the symmetrical location at the opposite side of the room (Fig. 2), providing evidence that they reoriented by means of an encapsulated system operating on a geometric description of the surface layout.

Although fish, birds and primates reorient primarily by the shape of their surroundings, their foraging performance is also influenced by non-geometric information [27–29]. Moreover, disoriented rats navigate in accordance with non-geometric landmark features when they are tested in a highly motivating escape task [31] or in a familiar environment [32,33]. These findings suggest that the navigation performance of disoriented animals is enhanced by the view-dependent scene

representations discussed in the previous section: when a disoriented animal detects that two corners of its rectangular environment are congruent with the location at which it searched for food, it can choose between these locations on the basis of their match or mismatch to scene representations that were stored in memory before disorientation [13]. Note, however, that disoriented animals do not navigate by such landmarks as robustly as oriented animals do [32]. View-dependent scene representations may be most useful when an animal senses that it is close to the expected scene [13].

Summary

Animals with cognitive systems as simple as insects navigate by continuously updating the vectors specifying their relation to significant environmental locations such as the nest. As they do so, animals store egocentric representations of significant places for recognition, and they use these representations on trips through familiar territory, falling back on their path integration system when they wander into novel terrain. Finally, a variety of animals among fish, birds and mammals reorient themselves primarily by the geometry of the surrounding surface layout.

The representations constructed by these mechanisms differ in three ways from the maps constructed by human geographers. First, maps are enduring, but the path integration system yields a representation that is continuously changing: it specifies environmental distances and directions from the animal *at that moment*, rather than timeless spatial relationships. Second, maps are geocentric, but the representations that underlie place recognition are egocentric: they specify the appearance of landmarks from the vantage point of the navigating animal, rather than the distances and directions of all places in the environment from one another. Third, maps are unitary representations, but none of the mechanisms found in animals gives rise to a unitary representation of all perceptible features of the environment. In particular, the reorientation system represents only the shape of the permanent, surrounding surface layout. These differences raise pointed questions about human navigation.

The navigation system in humans

Although the human brain and cognitive system is far more complex than that of any other animal, humans may have inherited much of the same machinery that is found throughout the animal kingdom and that guides navigation in a wide variety of species. The navigation systems of ants, rodents and humans might also have converged over evolution in response to similar ecological demands, as all these species are central place foragers. In this section, we ask whether human navigation is guided by the three processes discussed above: path integration, view-dependent scene recognition and geometry-based reorientation.

Path integration

Like other animals, humans can return to the origin of a path [34–36] (Fig. 1) and travel to familiar locations along novel paths [37,38]. Do these abilities depend on an allocentric cognitive map of the environment [1–3,13] or on a path integration process? In principle, humans could pursue novel short-cut routes among multiple objects by continuously updating their relationships to each object as they move, in the same way that ants update the homing vector. By increasing the number of vectors updated, a path integration system can flexibly guide the navigator to a multitude of locations along novel paths.

Timeless, allocentric spatial representations can be distinguished from dynamic egocentric spatial representations by investigating memory for a configuration of targets as the navigator moves.

Whereas an allocentric map remains the same as the navigator travels, an egocentric representation is updated continuously. With noise in the updating process, the configuration of the vectors will change over time and the original configuration will be unrecoverable. Accordingly, we tested subjects' memory for a configuration of object locations under different conditions of motion and disorientation [39]. Subjects learned the locations of six surrounding objects, pointed to the objects while blindfolded (baseline condition), disoriented themselves by turning, and then pointed to the objects again (disoriented condition). Error in the relative pointing responses to different targets ('configuration error') was measured. Consistent with the dynamic updating hypothesis, configuration error increased after disorientation (Fig. 3). By contrast, subjects showed no increase in configuration error when the experiment was repeated with the addition of a single directional light that allowed subjects to maintain their orientation as they turned (Fig. 3, oriented turning), providing evidence that the increased error in the disorientation condition was not caused by memory or performance factors and was instead associated specifically with the subjects' loss of orientation.

Finally, we tested whether the configuration of the targets was recoverable after disorientation by following the same procedure as in the oriented turning condition except during turning, when the light was extinguished and subjects became disoriented. When the light was turned back on, subjects were able to reorient themselves, but their configuration error was as high as in the original disoriented condition and higher than in the oriented turning condition (Fig. 3, reoriented). Pointing evidently was not guided by an enduring, allocentric cognitive map, for such a map should be available to reoriented subjects as well as to continuously oriented ones.

Do these results imply that humans have no enduring, allocentric representations of their

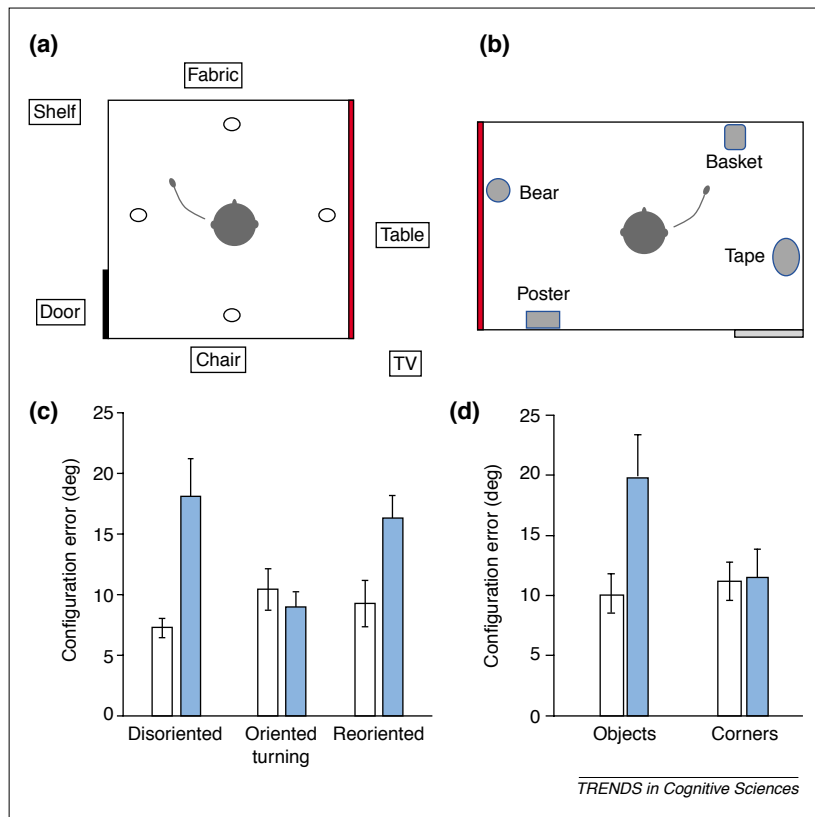


Fig. 3. The egocentric updating system and representations of environment geometry in humans. Subjects first learned the locations of objects and were then blindfolded. In each experiment, the subject sat on a swivel chair in the center of the room and pointed to the targets. (a) The square room with six surrounding targets. Four lights (ellipses) were mounted on the ceiling illuminating the room; one light served as the directional cue with the other three switched off. A video camera was mounted at the center of the ceiling directly overhead to record the subjects' pointing responses. (b) The rectangular room with four objects placed near the walls; the objects were arranged in the same angular configuration as the four corners of the room. Again a swivel chair was placed in the middle of the room, on which the subjects sat and pointed to the corners or the objects. As a measure of the internal consistency in pointing to multiple targets, configuration errors were calculated as the standard deviation of the mean angular pointing errors of the individual targets. These are shown for the disoriented, oriented-turning and reoriented conditions for the task of pointing to six objects (a,c) and for the tasks of pointing to objects versus corners (b,d), both before (baseline, open bars) and after rotation (test, blue bars). (Redrawn from Ref. [39].)

surroundings? The studies of animal navigation reviewed above provide evidence for one such representation – a representation of the shape of the surrounding surface layout that survives disorientation and allows animals to reorient themselves [30]. Our last experiments [39] tested for the same representation in humans by having subjects point both to the corners of a chamber and to an array of objects forming the same angular configuration as the corners, both before and after disorientation. Subjects showed increased configuration error in the objects task but not in the corners task (Fig. 3), suggesting that the shape of the surface layout is encoded in an enduring, allocentric representation. Except for this representation, however, the dynamic path integration system seems to be as fundamental to human navigation as it is to the navigation of ants and bees.

View-dependent place recognition

Like insects, humans use view-dependent representations to recognize objects and places [40–49].

For example, when subjects are shown an object array on a circular table and then judge whether pictures taken from various vantage points present the same array, their response latency is a linear function of the angular distance between the test view and the studied view [41,49]. When an array is studied from more than one vantage point, moreover, recognition performance is best at the studied views and becomes progressively worse as the test view deviates further from the nearest studied view [41,49]. These findings provide evidence for view-dependent representations of scenes.

Similar findings emerge from studies in which people learn to navigate through a virtual neighborhood of interconnecting streets furnished with multiple landmarks. Patterns of travel provide evidence that people learn to turn in specific directions at particular places [50], and that their turning decisions depend on local, view-dependent representations of landmarks rather than on global representations of the scene [51]. Finally, studies of patients with unilateral neglect provide evidence that even highly familiar scenes are stored in view-dependent representations. Asked to imagine a city square while facing east, such a patient may report only the buildings to the south; asked then to imagine the same square while facing west, the patient will report only the buildings to the north. In both cases, neglect of the left side of egocentric space provides evidence for view-dependent representations of the layout [52].

Recent studies reveal that humans update these viewer-centered representations during locomotion. Wang and Simons [53] showed subjects an array of objects on a circular table and then tested their ability to detect a moved object in the array after movement of themselves or the table. When subjects remained at the study position, performance was better when the table remained still than when it was rotated, suggesting that recognition of a real world scene is view-specific (Fig. 4). When subjects were tested at the new position, however, they performed better when the table remained still, presenting a novel view of the array, than when it rotated with them and presented the familiar view [53]. The same results were obtained when subjects actively rotated the table or were passively wheeled to the new observation point [53]. Finally, subjects' ability to recognize the scene was impaired when they were disoriented between study and test [54]. These findings provide further evidence that subjects update egocentric representations of object arrays during locomotion, and that updating is disrupted by disorientation.

Reorientation

Although the experiments described above provide indirect evidence for a geometry-based reorientation system in humans [39], more direct evidence comes from experiments presenting adults and young

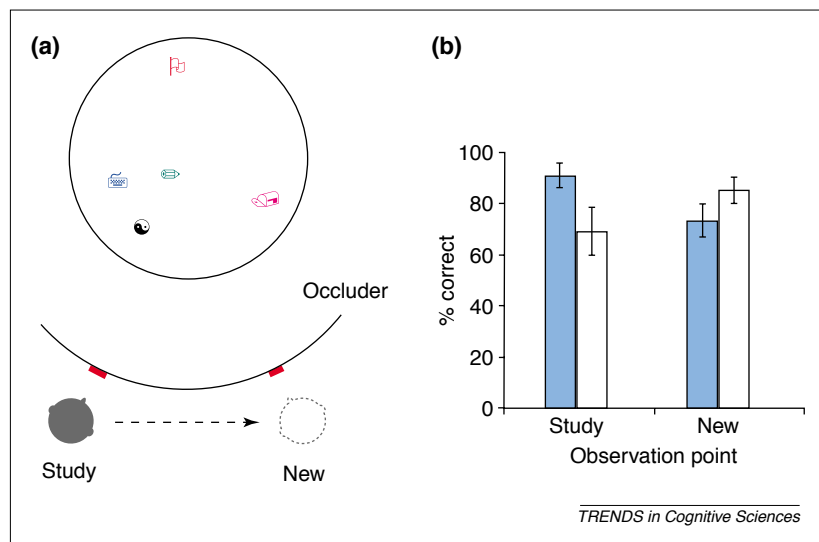


Fig. 4. The updating of view-dependent scene representations in humans. (a) Subjects studied the object array on a circular table and were tested either at the study position or after walking to a different position 40° around the table ('New'). The test was then either with the same view of the object array as the studied view or with a 40° rotated view. (b) Subjects' accuracy in detecting a moved object in the array from both test positions, either when the view matched that initially observed (blue bars) or when it was different (open bars). Accuracy was higher when the table position remained the same as during initial observation, even though this meant a novel view from the new observation point. (Redrawn from Figs 1 and 2 in Ref. [53].)

children with a variant of Cheng's navigation task. In one series of studies [55], 1.5- to 2-year-old children saw a toy hidden in one corner of a rectangular chamber, were disoriented by turning, and then 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 or by the presence of a distinctive landmark object. Like rats, children searched reliably and equally at the correct corner and at the geometrically equivalent opposite corner (Fig. 2). Their successful use of room geometry showed that they were motivated to perform the task, remembered the object's location, and, like rats, reoriented in accordance with the shape of the surface layout but not by non-geometric landmarks.

Further experiments revealed that children's failure to reorient by non-geometric information extends to square or circular rooms [56,57], is specific to the task of reorientation [55,56], and does not stem from any failure to detect or remember the landmarks [56]. Experiments also provide evidence that the representation guiding children's reorientation captures information about the shape of the surface layout but not about the shape of a configuration of objects [57]. Finally, disoriented children, like animals, do rely on non-geometric information under certain conditions: they search in the correct relation to a distinctively colored wall if they are tested in a large room [58], and they search correctly when the hiding location has unique distinguishing properties such as a unique color or pattern [57]. Children, like rats, might therefore use view-specific scene representations to select among geometrically equivalent locations.

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All of the above studies were conducted with young children, and so they raise the question whether human adults possess the same encapsulated reorientation system. Adults tested in Hermer's task successfully located an object in accordance with both the shape of the room and a non-geometric landmark [55]. Some subjects used egocentric spatial language to describe the landmark information, reporting that an object was hidden 'in the corner with a blue wall on the left'. Developmental studies revealed that the transition from encapsulated to flexible performance correlated with the acquisition of these spatial terms and expressions [59]. To investigate the effects of verbal encoding on adults' navigation and the existence of a language-independent geometric reorientation system, experiments investigated adults' performance in this reorientation task under conditions of verbal and nonverbal interference [60]. Although nonverbal interference led to an overall degradation of performance, human adults continued to use both geometric and landmark information. By contrast, verbal interference suppressed adults' ability to locate the object in relation to the landmark, while sparing their ability to locate the object in relation to the shape of the room. These findings provide evidence that the geometric reorientation system found in rats and in human children is present and functional in human adults. Under normal conditions, however, this navigation system is supplemented by a different system of representation that captures landmark information and depends in some way on human language.

Conclusions

How do humans find their way from place to place? If psychologists take intuition as our starting point, then we may focus on humans' striking and salient use of maps and propose that the building blocks of human navigation are internalized versions of these symbolic representations – cognitive maps. Studies of animal navigation nevertheless suggest a different view. Although the maps that human geographers design are enduring, geocentric, and all-embracing in their scope and flexibility, the internal representations that guide human navigation have none of these properties. Like many animals, humans navigate by forming, maintaining, and dynamically updating a representation of their momentary relationship to significant environmental locations. Humans also recognize objects and scenes by matching the current visual field to stored, view-specific representations of places. Finally, humans reorient themselves when their path integration system is disabled by analyzing the shape, but not other properties, of the surrounding layout. In all these cases, the findings of experiments on human navigation clash with human intuition and accord to a surprising degree with the findings of experiments on navigation in non-human animals.

If all navigation abilities build on a common set of mechanisms, then we may rephrase our initial question about human uniqueness: What enables humans to go beyond the limits of these systems so as to navigate more flexibly? Studies of the phylogeny and ontogeny of human navigation provide an approach to this question and hint at an answer. Coordinated studies of animals and human infants suggest that the building blocks for these capacities are a set of encapsulated representations of the

environment. Studies of developing children and adults suggest that humans come to construct new spatial representations and navigational strategies by drawing on specifically human symbolic capacities. From these hints may come specific, testable hypotheses about the mechanisms by which humans overcome the limits of our primitive navigational systems and create systems of representation that are unique in the living world – truly geocentric maps of the environment.

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Depth of processing in language comprehension: not noticing the evidence

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The study of processes underlying the interpretation of language often produces evidence that they are complete and occur incrementally. However, computational linguistics has shown that interpretations are often effective even if they are underspecified. We present evidence that similar underspecified representations are used by humans during comprehension, drawing on a scattered and varied literature. We also show how linguistic properties of focus, subordination and focalization can control depth of processing, leading to underspecified representations. Modulation of degrees of specification might provide a way forward in the development of models of the processing underlying language understanding.

Experimental research on human language processing has repeatedly demonstrated that the various sub-processes occur extremely quickly [1–3]. Perhaps because of the concentration on individual sub-processes, many researchers implicitly assume that these processes are not only initiated quickly, but are also completed quickly, resulting in the fast and dynamic construction of a fully articulated analysis of the linguistic input at each level. However, the time-course of processing and the depth of processing represent two orthogonal dimensions, and we currently know far more about the former than the latter.

In this article, we suggest that many processes are incomplete, and that interpretations are not as full as possible, but are often 'underspecified'. Recent work in computational linguistics and formal semantics has highlighted underspecification, which allows processing to proceed without maintaining a full analysis. Also, a variety of results in psycholinguistics show that language processing can be shallower than is commonly assumed. We shall argue that during comprehension, each word in a sentence does not necessarily contribute its full meaning, and these meanings are not always combined into

higher-level phrase meanings through a fully determinate analysis.

Our case is that underspecification has a major role to play in the further development of process models of language comprehension. In fact, fully specified interpretations of language can often seem both undesirable and unnecessary. For instance, consider the pronouns in the following sentences:

(1) *Mary bought a brand new Hitachi radio.*
 (2) *It was in Selfridge's window.*
 (3) *Later, when Joan saw it, she too decided it would be a good purchase.*

A full specification of the referent of *it* in (2) is not possible. Did Mary buy the particular radio that was physically in the window, or was the one in the window just an exemplar of the set of radios? The interpretation of *it* in (3) offers even more possibilities. This example shows that processing might not occur to a fine grain. Indeed, it has been argued that there are many cases where the referent of a pronoun cannot be determined, and yet people are not concerned about this fact. Another example of an unresolved pronoun comes from the TRAINS corpus collected at the University of Rochester. The corpus is of dialogs about about train scheduling:

A: *'can we kindly hook up....uh...engine E2 to the boxcar at Elmira'*

B: *'okay'*

A: *'and send it to Corning as soon as possible please'*

B: *'okay'*

The pronoun *it* in the penultimate line is unresolved because it is ambiguous as to whether it refers to the engine, the boxcar, or both [4]. However, in this example, because the result of sending *it* to Corning remains the same, the referent of *it* may remain underspecified without affecting the key interpretation. The general question in these cases is whether or not a particular interpretation has been given, or whether some less specific representation has been formed.

Shallow processing in computational linguistics

Recent work in computational linguistics has used underspecified representations of text. So, although full parsing aims to recover a fully articulated grammatical structure for a sentence, 'shallow parsing' [5], aims simply to identify non-overlapping 'chunks' of structure in a text (Fig. 1). Choosing whether to build a full or shallow parser depends on how one wishes to use the resulting representations. For some tasks (e.g. automatic generation of indexes for large texts), shallow parsing is sufficient, whereas others (e.g. machine translation) require fuller analyses.

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