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Spatial memory: how egocentric and allocentric combine

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Recent experiments indicate the need for revision of a model of spatial memory consisting of viewpoint-specific representations, egocentric spatial updating and a geometric module for reorientation. Instead, it appears that both egocentric and allocentric representations exist in parallel, and combine to support behavior according to the task. Current research indicates complementary roles for these representations, with increasing dependence on allocentric representations with the amount of movement between presentation and retrieval, the number of objects remembered, and the size, familiarity and intrinsic structure of the environment. Identifying the neuronal mechanisms and functional roles of each type of representation, and of their interactions, promises to provide a framework for investigation of the organization of human memory more generally.

Introduction

The nature of the representations underlying human spatial cognition has long been the subject of intense debate [1]. Four years ago, an influential opinion piece [2] suggested that spatial memory was solely supported by 'egocentric' representations of location (i.e. centered on parts of the body), together with a representation of the surface geometry of the environment that enables the reorientation of a disoriented individual. This simple model inspired several experiments in cognitive psychology. Here, I review some of these recent results and show how, together with neuroscientific evidence regarding the nature of spatial representation in the brain, they reveal the parallel presence of both egocentric representations and 'allocentric' (or 'geocentric') representations centered on aspects of the external environment. Further, these results begin to illuminate the complementary contributions to cognition made by egocentric and allocentric representations, and the ways in which they interact.

It has often been argued that the presence of allocentric representations cannot be safely inferred from behavioral results because alternative explanations using solely egocentric representation can often be found [3]. Building upon several elegant experimental findings from their own and other laboratories, Wang and Spelke [2] suggested a simple model of spatial memory that depends upon two types of egocentric process and a 'geometric module' [4,5]. The egocentric processes are viewpoint-dependent scene recognition and spatial updating of egocentric locations by self-motion information. The geometric module represents the surface geometry of the surrounding environment, and is used for reorientation of disoriented individuals, but has no direct role in representing object locations. Enduring allocentric representations of location are explicitly absent. Alone among mammals, they argue, humans can go beyond these basic processes by using natural language to combine each with the other, as well as by using artifacts such as symbolic maps.

Evidence for an egocentric model

The model of Wang and Spelke was supported by four main strands of evidence, briefly reviewed below.

Alignment effects

The existence of viewpoint-dependent representations of the visual scene has been indicated by several studies in which an array of objects is studied from a specific viewpoint. The time taken to recognize photographs from other viewpoints around the array increases linearly with the difference in angle between the two viewpoints [6]. When people are asked to point to an object from an imagined viewpoint, they are faster and more accurate when the imagined viewpoint has the same direction as the studied viewpoint [7] (Figure 1, 'egocentric axis'). These results indicate storage of a viewpoint-dependent representation of the visual scene, followed by some sequential process of mental rotation (for recognizing a photograph), or mental navigation (for imagining new viewpoints).

Spatial updating

An elegant paradigm, in which people detect which of five objects on a circular table has been moved, provides evidence for representations of object locations that are updated by self-motion [8,9] (see also Ref. [10]). In four conditions, the person either moves to a new viewpoint or not, and the table is either rotated or not in the gap between study and test. The test array will be consistent with viewpoint-dependent representations if both viewpoint and table are rotated together; with self-motion updated representations if the viewpoint alone is rotated; with both types of representation if neither is rotated; and with neither type of representation if the table is rotated alone. The results indicate a strong effect of motion-related spatial updating and a weaker effect of viewpoint dependence (Figure 2, conditions _, P, T, PT).

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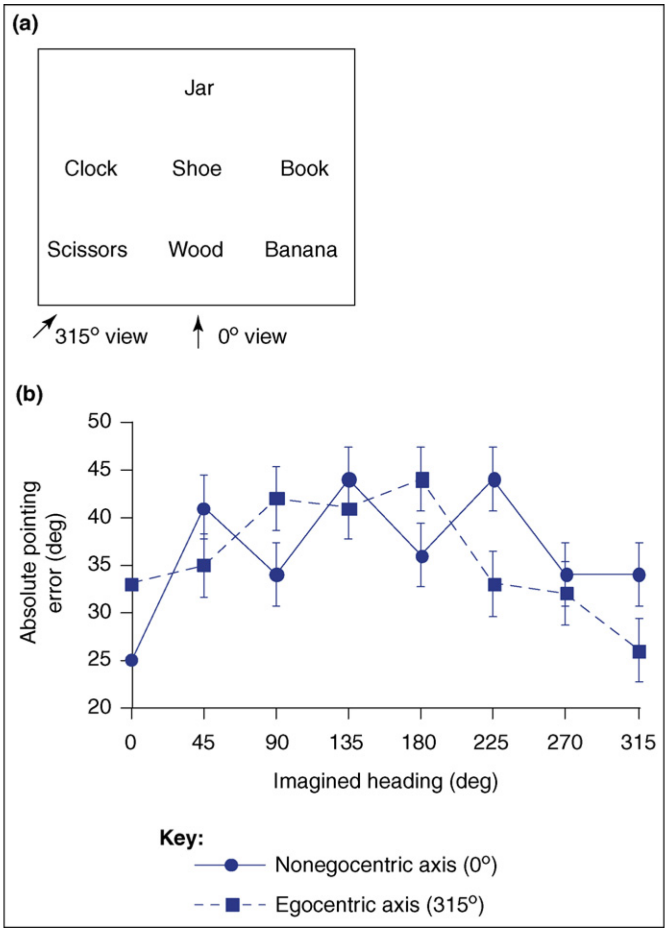

Figure 1. Alignment effects [31]. **(a)** Participants viewed an array of objects from a 315° view. One group (the 'nonegocentric' group) learned the objects in columns along the nonegocentric 0° axis (i.e. scissors–clock, wood–shoe–jar, banana–book), the other ('egocentric') group learned the objects along the egocentric 315° axis (i.e. clock–jar, scissors–shoe, wood–book, banana). **(b)** Both groups made judgments of relative directions between objects from imagined viewpoints, based on their memory for the array. The nonegocentric 0° group performs more accurately when imagining novel viewpoints aligned with the 0° axis than with the original 315° viewpoint. They also perform better when imagining other views aligned with the intrinsic axes of the array (90°, 180°, 270°) than aligned with other directions. The egocentric 315° group perform best when imagining viewpoints aligned with the familiar 315° viewing and learning direction, with performance decreasing for novel viewpoints as a function of their difference from 315°, replicating previous findings supporting egocentric representations. Adapted, with permission, from Ref. [31].

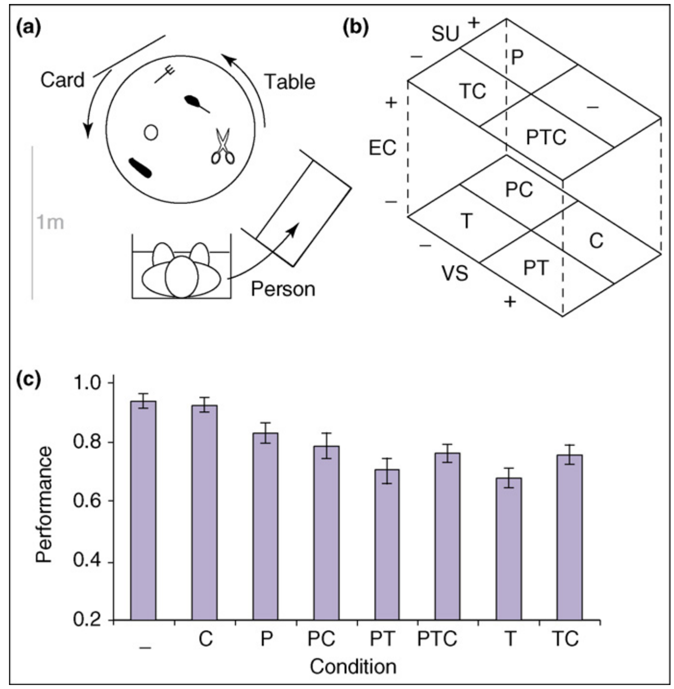

Figure 2. Consistency with visual snapshots, spatial updating and an external cue [33]. **(a)** Participants view an array of five phosphorescent objects on a round table and a phosphorescent card (the external cue) in the dark. After a brief delay, they are asked to indicate which of the objects has been moved. **(b)** Between viewing and test, the person (P), table (T) or card (C) might move so that the test configuration is consistent (+) or inconsistent (–) with stored visual snapshots (VS), representations spatially updated (SU) by self-motion, or the external cue (EC), in a $2 \times 2 \times 2$ factorial design. Abbreviations: PT, person and table; PTC, person, table and card; TC, table and card; PC, person and card. **(c)** Performance (shown as proportion of trials correct) indicates significant beneficial effects of consistency with all three types of representation. Conditions corresponding to no change (_), and movement of P, PT and T replicate the effects of consistency with SU and VS found by Wang and Simons [8]; the additional effect of the EC can be seen in the other four conditions (helping when it moves with the T, PTC versus PT, TC versus T; hindering when it moves without the T, C versus _, PC versus P). Error bars show the standard error of the mean. Adapted, with permission, from Ref. [33].

Pointing errors

A study by Wang and Spelke [11] involved subjects learning the locations of objects scattered around a room, followed by the experimenter asking them to point to the objects while sitting on a swivel chair in a chamber in the centre of the room. Responses were made with eyes open, blindfolded and blindfolded after disorientation by rotating the chair. The error in blindfolded pointing is found by comparison to pointing in the preceding eyes-open condition. They found that disorientation before pointing greatly increased the variation across objects in pointing errors, even when taking into account any increased variation across trials in pointing to the same object (Figure 3, 'pointing'). This result indicates the presence of egocentric representations of object locations that are individually reset after disorientation, and do not provide any evidence for a holistic representation of all objects upon which disorientation should produce a fixed offset for all objects. However, unlike pointing to objects, they found no increase in the variability of errors in pointing to the corners of the room.

Reorientation

When an animal is disoriented (e.g. by several rotations in the absence of stable sensory cues), it must reorient itself with respect to the surrounding environment before it can navigate to a remembered location. Following similar experiments with rats [12,13], Hermer and Spelke [14,15] showed that preverbal human infants reorient themselves using the geometry of the surrounding walls when searching for a toy in a small rectangular room (searching in the correct corner and also the opposite, geometrically equivalent, corner), despite the presence of a polarizing visual cue (one blue wall). By contrast, they searched correctly when a polarizing geometric cue was present [16]. They also found that adults made similar 'geometric' errors when performing a demanding concurrent verbal task but not when performing a concurrent nonverbal task [17] (Figure 4a). Thus, environmental geometry has a privileged role in reorientation, to the exclusion of other types of information, at least in the absence of linguistic processes. Conversely, in the model of Wang and Spelke, the encapsulation of geometric information also

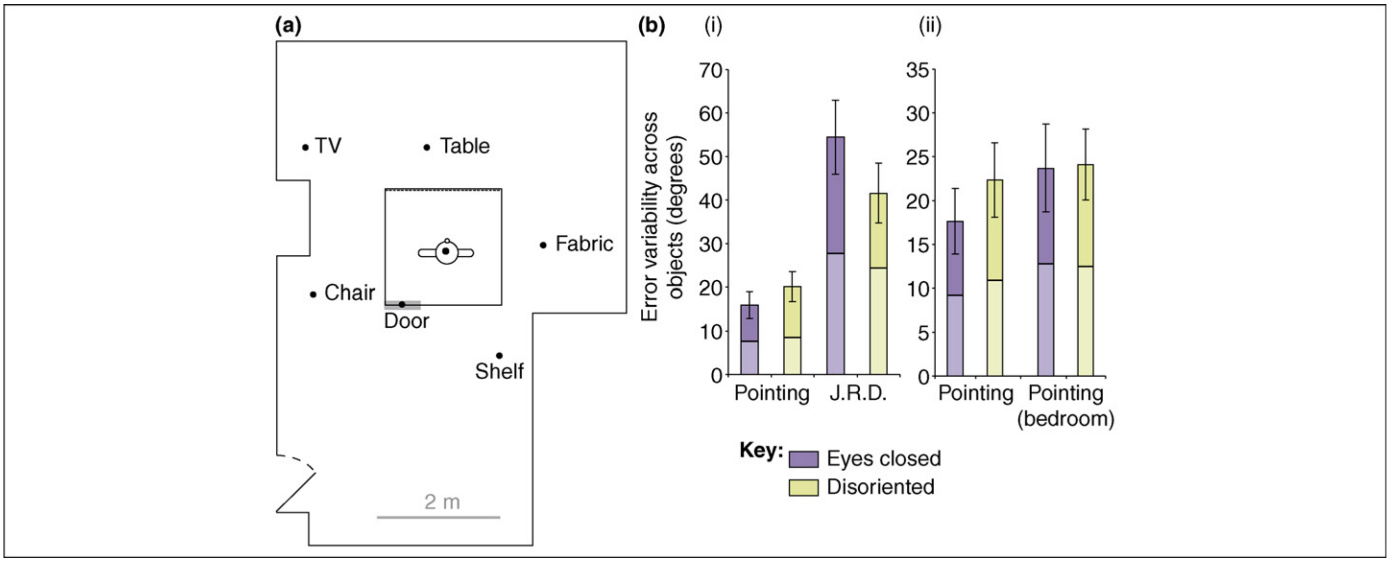

Figure 3. Variability of pointing errors after disorientation. **(a)** Participants learn the locations of objects in the outer room, then enter the inner chamber, where they sit on a rotating stool and perform pointing tasks with their eyes open, blindfolded and following disorientation (rotation on the stool, blindfolded). **(b)** Participants either point to the location of an object (Pointing) or to where an object would be from an imagined viewpoint specified in terms of two other objects (a judgment of relative direction, J.R.D.). (i) Error variability across objects increases with disorientation in the pointing task, replicating the effect found by Wang and Spelke [11], but decreases in the judgment of relative direction task. (ii) The increase in error variability in pointing is replicated in the laboratory setting but no such effect occurs when subjects point to the imagined locations of objects in their bedroom. The lower portion of each bar indicates the proportion of error variability across objects due to the variability in pointing over trials with the same object. Error bars indicate 95% confidence intervals. Adapted, with permission, from Ref. [34].

prevents it from being used with other types of (egocentric) information to represent object locations.

Egocentric and allocentric representations exist in parallel

The model of Wang and Spelke raised several questions. First, although much evidence for egocentric representations was presented, this does not constitute evidence for the absence of allocentric representations. Direct evidence for or against representations centered on some aspects of the environment requires experimental manipulation of the environmental cues.

Second, although a mathematically equivalent egocentric frame of reference exists for any allocentric frame

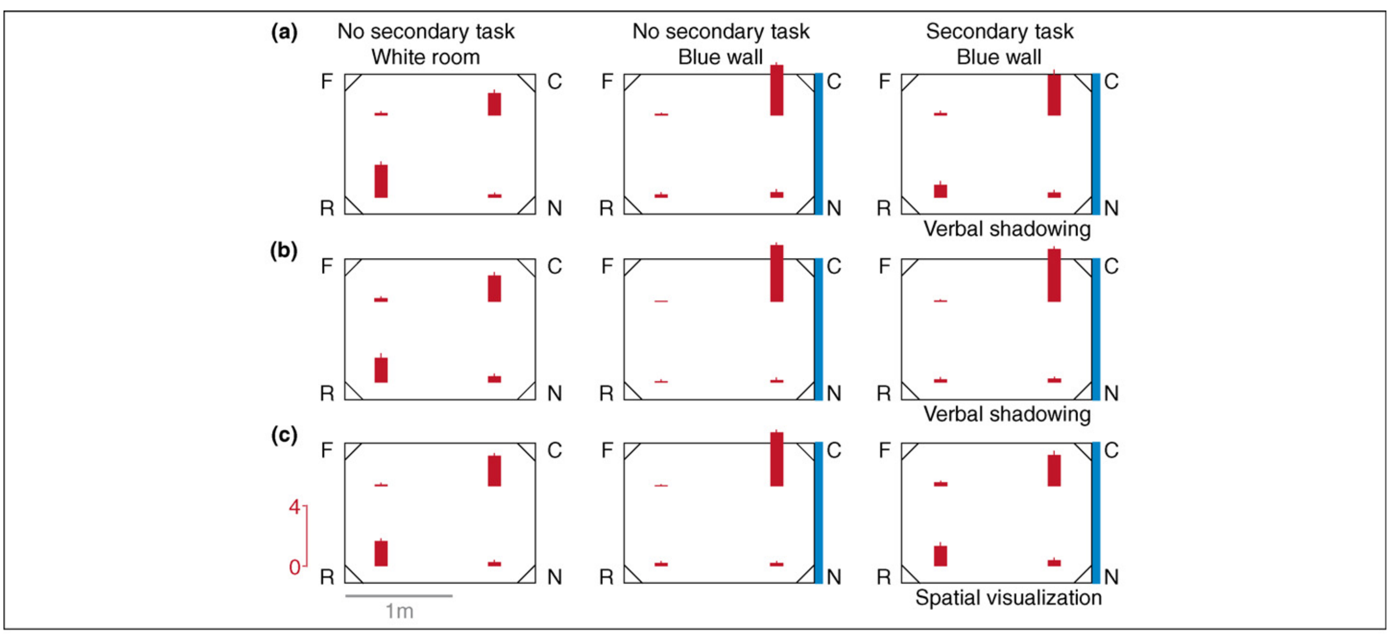

Figure 4. Reorientation in adult humans [43]. Participants see an object being hidden in a corner of a small rectangular enclosure, are disoriented by rotation and then asked to point to the object. The correct corner (C) and initial facing direction are counterbalanced. Other corners are labeled relative to the correct one as rotationally equivalent (R), near (N) and far (F). The enclosure can have all white walls, or one blue wall. **(a)** In a replication of Hermer-Vazquez *et al.* [17], participants were told: 'You will see something happening that you should try to notice' and that they would be asked about what they saw. They then practiced verbal shadowing (immediately repeating text heard through headphones) and, still shadowing, performed four trials with the blue wall, stopped shadowing and performed four more trials with the blue wall and four trials with all white walls. Performance (red bars: mean number of searches per corner and standard error) shows equal levels of responding in C and R corners in the white room, correct responding with the blue wall, but raised R errors when shadowing, despite the blue wall. **(b)** When participants are given more complete instructions and a practice trial, and the order of conditions is counterbalanced, they do not show significantly raised R errors when shadowing with the blue wall present. **(c)** When participants, instructed as in (a), perform a concurrent spatial visualization task, raised R errors can be seen in the blue wall condition, similar to the case with verbal shadowing. Adapted, with permission, from Ref. [43].

of reference, maintaining an egocentric representation becomes increasingly daunting as distances and numbers of locations increase. Thus, a simple forward movement requires different individual changes to the egocentric locations of every object in the environment but changes only self-location within an allocentric environmental representation. Equally, the relative locations of familiar places in your neighborhood which cannot all be seen from a single viewpoint can be imagined from an arbitrary (possibly moving) viewpoint while you holiday in another continent. This would be impossible using viewpoint-dependent scene recognition or egocentric representations updated by self-motion during your flight. Even extending the model to include an enduring representation of locations requires that this representation be accessible from any viewpoint. To do this correctly means that it must contain the relative locations of all potential viewpoints – that is, an allocentric representation by another name.

Third, in addition to the egocentric representations of location present in the parietal lobe and viewpoint-dependent representations of the visual scene throughout the 'ventral visual processing stream' [18], the mammalian brain also appears to support some allocentric representations [19]. Thus, representations of the subject's absolute location ('place cells') [20] and orientation [21] relative to the surrounding environment can be seen in rats and in monkeys [22,23]. Place cells have also been reported in humans [24] and viewpoint-independent representations of locations in the visual scene have been seen in monkeys [25] and humans [24]. Behavioral responses in spatial memory tasks reflect the representation of location of the place cells [26–28]. This representation is oriented by distant visual landmarks and otherwise determined by the distances from environmental boundaries [29]. Recent self-motion information is thought to update the represented location [30], and can dominate over visual cues if these are seen to be unstable or if the rat is systematically disoriented.

Inspired in part by these questions, several recent experiments have revisited the four main lines of support proposed for the egocentric model. Below, I outline their main findings, and why they imply revision of the egocentric model.

Alignment effects

In recent experiments, researchers have begun to find effects of alignment with directions defined by aspects of the external environment, as well as those defined by the person's initial viewpoint. When an array of objects contains an intrinsic axis (e.g. defined by symmetry or the sequence in which items are learned), but is not viewed along that direction, improved accuracy is found when pointing to objects from imagined viewpoints that are aligned with this axis, an effect that is strengthened when an intrinsic axis is also aligned with the testing room walls [31]. In these tasks (also known as 'judgments of relative direction'), the person imagines standing at one object, facing a second and pointing to where a third would be (Figure 1). When people learn the locations of objects while following a route through a park which encircles a large rectangular building, improved accuracy is found when pointing to objects from imagined viewpoints aligned with a salient landmark (e.g. a large lake), even when this viewing direction was not experienced. In addition, improved accuracy was found for viewpoints aligned with the legs of the route but only when these were arranged parallel to the walls of the central building [32]. Thus, in addition to egocentric representations, the locations of objects might also be stored in representations oriented with respect to landmarks or intrinsic axes in the external environment.

Spatial updating

The evidence for spatial updating [8,9] – that is, improved performance when test arrays are consistent with representations updated by self-motion – is potentially confounded with evidence for allocentric representations. Whenever object locations are consistent with representations updated by self-motion, they remain stationary within the testing room and are thus also consistent with any representations centered on the environmental cues within it. A contribution of spatial updating is not in doubt because the effect is diminished by disorientating the person during their movement to a new viewpoint, and is present (albeit somewhat reduced) when the experiment is performed in the dark with fluorescent objects so that the room cannot be seen [9]. Nonetheless, some of the effect ascribed to spatial updating might be due to allocentric representations.

A revised spatial updating experiment [33] examined the effects of consistency with viewpoint-dependent, spatially updated and allocentric representations within a $2 \times 2 \times 2$ design (Figure 2). People viewed an array of fluorescent objects and a fluorescent external cue in darkness, and subsequently indicated which object had moved. Between presentation and test, either the viewpoint array or cue could be rotated to manipulate the consistency of the test array with either type of representation. As well as replicating the effects of consistency with viewpoint-dependent and spatially updated representations (in the conditions in which the cue did not move), an effect of consistency with representations oriented with the external cue was also found. Performance increased when the card and table moved together and decreased when one or other moved alone, indicating a role for the external cue in object location memory.

Pointing errors

Increased variation in pointing error following disorientation is consistent with egocentric representations of individual object locations which are independently disrupted by disorientation. However, an alternative two-system interpretation was recently proposed by Waller and Hodgson [34]. They suggest that precise but transient egocentric representations of individual object locations exist in parallel with an enduring and more comprehensive representation of the array of objects. The enduring representation will be relatively coarse in a novel environment but might increase in accuracy with experience. In their view, the effect of disorientation is to cause a switch from the use of the precise transient representation to the coarse enduring one.

To support their view, Waller and Hodgson replicated the Wang and Spelke [11] result but showed that, whereas the variation in error when pointing to individual objects increases after disorientation, variation in the error when making judgments of the relative direction between objects actually decreases (Figure 3). This pattern is consistent with switching from a precise egocentric representation to one that is coarse (hence the reduced accuracy of pointing to single locations) but more comprehensive (hence the improved accuracy in judgments of relative direction). They also showed that, with a very familiar environment, pointing error variability does not increase with disorientation, consistent with the use of a comprehensive enduring representation both before and after disorientation. Finally, they showed that the 'disorientation' effect on pointing error variability in an unfamiliar environment occurs after a single rotation of 135°, indicating a switch between two representations rather than an effect of complete disorientation.

Consistent with the two-system interpretation, which predicts that disorientation only affects pointing error variability when it causes a switch between two systems of different accuracy, the increased variability occurs in some circumstances but not in others [35,36]. Variability does increase after disorientation when a small irregular array of objects (e.g. four or five) is viewed from within but does not when a larger number of objects is used, or the array is viewed from the edge [35]. Mou *et al.* [35] suggest that the external viewing, large numbers of objects and the presence of intrinsic spatial organization in the object array are all conducive to the use of an allocentric object–object representation, even before disorientation. Use of an allocentric representation before disorientation would also explain the absence of a disorientation effect on pointing to room corners [11] or pointing in a familiar large-scale environment [36], consistent with roles for intrinsic spatial structure and familiarity in inducing the use of allocentric representations.

Reorientation

Environmental geometry undoubtedly has a strong role in reorientation. However, many have queried the interpretation of a geometric module whose output, aside from enabling reorientation, can only be combined with other types of information via natural language [2,17]. For example, well-oriented rats routinely combine visual features and environmental geometry to locate objects [26,37]. In addition, the rats in the original reorientation study learned to search correctly if the bait was consistently placed in the same corner over many trials [12], as can chicks [38] and monkeys [39] (although human infants do not learn to do this over four such trials [15]).

Geometric-only reorientation is only found in specific situations. Infants correctly combine geometry and visual features in larger rectangular [40] or rhombic [41] rooms. Interestingly, the balance between using geometric or visual features varies similarly with environmental size in non-humans too [42]. Adults correctly combine these features while performing verbal shadowing if the task is explicitly explained and the order of shadowing and non-shadowing conditions counterbalanced [43]. In addition, spatial interference tasks can be as effective as verbal shadowing in raising the levels of geometric errors [4,43].

Thus, the picture of a necessarily encapsulated geometric module that can only combine with other modules via natural language is not supported in general. This realization reopens intriguing questions, such as how are geometric and nongeometric sources of information combined to control behavior? Experiments in which both types of information are put into conflict indicate important roles for environmental size [42] and the number and consistency of the available cues [44].

Concluding remarks

The precision of Wang and Spelke's analysis [2] beautifully exposed several key issues in human spatial cognition, inspiring a succession of studies. As a result, we now have a more complete understanding of the underlying processes.

Two-system models

Recent experimental data indicate a 'two-system' model of parallel egocentric and allocentric representations in object location memory [34,45–47]. By contrast, Wang and Spelke's model [2] had an allocentric component that solely reflected the surface geometry of the environment and was excluded from contributing directly to object–location memory. Common among the two-system models are transient action-oriented egocentric self-object associations and more enduring representational allocentric object–object or environment–object associations. The enduring representations are variously thought to be organized in terms of the intrinsic axes of the array of objects [46,48], vectors to landmarks [49] or extended environmental boundaries [28], or other aspects of the environment and its geometry [5,20,45,50].

The egocentric-allocentric division might follow a well-established neuropsychological distinction between the dorsal and ventral visual processing streams [18,51], reflecting the patterns of neuronal firing in the medial temporal and intraparietal regions at the ends of these streams [19,20,47]. Of course, other systems also contribute to spatial memory, including the learned association of egocentric responses to single stimuli supported by the dorsal striatum [52], which might enable the correct response to be learned over repeated trials in reorientation paradigms [12,38,39].

The presence of multiple systems raises the question of how they interact. Waller and Hodgson [34] varied the amount by which a person was rotated between seeing the objects and pointing to them. An increase in pointing error variation occurred after 135° but not after 90° or less, indicating a switch from one system to the other, rather than a compromise. However, there are also reasons for egocentric and allocentric systems to cooperate. Whereas egocentric systems can be used alone, the egocentric nature of perception and imagery require that input to and output from allocentric systems are mediated by transient egocentric representations. Conversely, action-oriented egocentric representations must be derived from enduring allocentric representations following long or complicated self-motion. Both considerations imply a process of translation between the systems [47] (e.g. between environmentally defined north and south and body-referenced left and right), which will depend on the current or imagined heading direction. This potentially explains the role in recollection of Papez's circuit – along which cells coding for head direction are found [21]. Spatial updating can be seen as a continuous repetition of this translation between systems, if movement velocity is also taken into account [53] (see also Refs [5,20,34,44–46]).

This picture also implies operation of different representations over different timescales. Egocentric movement-related spatial updating is useful for maintaining the percept of a stable world from moment to moment but cannot ensure the correct alignment of spatial representations connected by a long path [54]. This is consistent with the lack of influence of 'path integration' in large-scale navigation [55], and its unreliability after a small number of rotations [56]. Nonetheless, people can become familiar with the layout of large-scale environments, as consistent with the construction over time of an enduring allocentric representation.

In summary, the experimental evidence proposed by Wang and Spelke to support a simple egocentric model for object–location memory [2] now appears to be more consistent with a two-system model in which egocentric representations exist in parallel to (rather than instead of) allocentric ones. The use of either type of representation appears to depend on factors such as the amount of self-motion between presentation and retrieval; the size and intrinsic spatial structure of the environment; and the extent of prior experience within it. The neural bases of these representations, what determines which of these controls behavior, and the nature of their interactions with each other remain exciting topics for future research (Box 1).

Box 1. Questions for future research

The identification of two classes of representation in spatial memory (egocentric and allocentric) raises several questions regarding their relationship to other proposed distinctions and mechanisms.

- How do they relate to different timescales of memory? Although both types of representation could be required in either short-term memory (STM) or long-term memory (LTM) for appropriate tasks (e.g. LTM of egocentric 'flashbulb' memories, or STM tasks tapping knowledge of spatial layout, such as judgments of relative direction), is there a tendency for LTM to abstract more compact allocentric representations from multiple independent egocentric representations, whereas egocentric representations generally suffice for short-term or 'working' memory [51]?
- How do they relate to more general categorizations of memory? Do allocentric representations in spatial memory provide a model for 'semantic' memory, in being abstracted over experience, or for 'relational' memory, being flexible in the sense of retrieval from novel viewpoints? Is procedural memory (e.g. as when following a well-learned route) always egocentric in nature, reflecting repeated associations between stimuli and physical responses?
- How do they interact with each other? Can we identify the translation between egocentric and allocentric representations during encoding of (egocentric) perceptual information into (allocentric) LTM and during retrieval from LTM into egocentric representations for imagery [47]? (N.B. Although the required translation could be as simple as a rotation from compass orientation to head-centered orientation in some circumstances, in others it might be much more complex – for example, producing an imaginable two-dimensional spatial layout from the allocentric knowledge of the distances between cities in the USA requires more processing [e.g. multidimensional scaling].)
- What are their neural bases? Does the hippocampus enable a viewpoint to be imposed on allocentric data stored in the medial temporal lobe for retrieval or imagery in parietal cortex [47,53]? Do retrosplenial areas mediate translation between these two systems? Can spatial updating of one's own viewpoint within an environment (e.g. implemented by entorhinal 'grid cells' [30]) be dissociated from egocentric spatial updating of the individual locations of objects around one (e.g. implemented in parietal cortex [19])?

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