The Mind's Views of Space

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Abstract

How does the mind understand space? This paper reviews some relevant findings and describes a unified theoretical framework for human spatial cognition called FORMS. The theory maintains that spatial cognition is an elementary brain function and involves multiple unique brain systems. Space is represented in the mind not once but multiple times, not unified but segmented. Each representation is a salience map with a distinctive frame of reference. It is believed that this theory has solid neuroscience support, is consistent with the general findings that the mind's views of space are often segmented, relative, and distorted, and provides a theoretical foundation for computational modeling of human spatial cognition.

Introduction

In a certain sense everyone knows what space is. It is the boundless extension of the field in which we, and everything else, physically reside and move around. However this is only the physical side of space. There is also a psychological side of space, which is about how the physical space is digested and represented in the brain and in the mind. Many spatial tasks, as simple as locating one's current position and finding a way back home, require us to maintain adequate internal representations of space.

While the physical space, with which we directly and indirectly interact, appears perfectly three-dimensional, absolute, unified, symmetric, and Euclidean, it is well documented that the psychological space differs from the physical space in many important aspects. A large body of evidence has shown that, regardless of how it is acquired – either through direct explorations or by means of spatial artifacts (e.g., maps, virtual reality, and language description) – psychological space is often distorted, relative, asymmetric, hierarchical, and segmented. How and why this is so remains elusive (for reviews, see McDonald & Pellegrino, 1993; Hunt and Waller, 1999; Tversky, 2000).

Much progress has been made in recent years towards partially resolving the puzzle. A large body of evidence, in the broad areas of psychology, cognitive neuroscience, and cognitive science, provides the much-needed details about how spatial information is processed and represented in the brain. These details, though often isolated in a specified domain, when taken together may lead to important understanding on both the brain foundations of spatial cognition and the computational nature of spatial information processing in the brain (e.g., Burgess, Jeffery, & O'Keefe, 1999).

It is the purpose of this paper to review some of the relevant findings about spatial information processing in the brain. We aim to show that these findings can be unified by the concept that spatial cognition is an elementary brain function and involves multiple distinct brain systems that are essentially "spatial". A theory of spatial cognition, called FORMS (Frame Of Reference-based Map of Salience), is then described based on this concept. This theory can potentially unify results and views from different perspectives and at different levels and permit a more complete and clarified understanding of how space is processed and represented in the brain and in the mind.

Spatial Cognition

People engage in spatial cognition in everyday life, ranging from locating their car key, reaching and grasping it, driving to work, and finding a way back home. Spatial information processing is critical to one's survival. However, the reason for spatial cognition as a distinct and elementary brain function is not obvious. Those tasks we typically called spatial tasks are generally not purely spatial but extensively involve perception, attention, general cognition, and motor components. Take a generic visually guided reaching task for example. To reach an object in the visual field it has to be a) located (e.g., relative to the direction of gaze), b) attended, c) recognized, d) relocated (relative to the arm), and e) reached through a set of motor commands. While steps b), c), and d) are of attention, vision, and motor control, respectively, steps a) and d) are of spatial information processing.

The notion that spatial cognition is a distinct and elementary brain function gains support from multiple aspects. Computationally (e.g., Marr, 1982), spatial cognition has a distinct computational goal: to construct internal representations of the external space by identifying important object-to-self and object-to-object spatial relations. Though closely related to vision, spatial cognition and vision achieve different computational goals. While vision has to collapse spatial dimensions to reach spatially invariant object recognition, spatial cognition has to emphasize the spatial relations. For example, suppose an apple falls from a tree to the ground. While vision recognizes that it is the same apple and affords similar edibility, spatial cognition notices that an object has occupied two different locations and it is now reachable. Understanding spatial relations is the distinctive computation achieved by spatial cognition. Neuropsychologically, patients with bilateral posterior parietal damage may accurately recognize an object but cannot point to it or describe its location relative to other objects in the scene. Conversely, patients with bilateral inferotemporal damage may perform well in solving spatial problems but fail to recognize objects, words, and faces. Similar dissociations have also been found in single neuron recording and neuroimaging data (see Farah, 2000 for a complete treatment). It is these observations that lead to the idea of two distinct cortical systems, with the dorsal "where" pathway specialized for spatial localization and the ventral "what" pathway for object recognition (e.g., Ungerlider & Mishkin, 1982). Finally, though spatial information often comes into the brain through a specific sensory channel, including visual, auditory, tactile, proprioceptive, and vestibular, these modality-specific inputs have to be integrated to achieve supramodal representations of space. Automatic visual fixation of the location of a sound is a common everyday experience and a good demonstration of cross-modality spatial representations. In addition, patients with unilateral posterior parietal damage show deficits in all modalities on the contralateral side of space, indicating the damage affects not any specific modality but the general spatial function.

The relation between spatial cognition and attention is an interesting one. Posner and colleagues argue that attention can be divided into three major functions, for alerting, orienting, and executive control, and that each function involves distinct brain networks (see Posner & Petersen, 1990; Fan, MaCandliss, Sommer, Raz, & Posner, in press). Obviously, the orienting function of attention is closely related to spatial cognition. Shifting attention from one location to another, either overtly or covertly, requires an encoding of the destination location relative to the origin, and this encoding is intrinsically spatial. It is surprising to see that the attentional network subserving orienting (parts of posterior parietal cortex, the frontal eye fields and such subcortical areas as superior colliculus and the pulvinar) is almost identical to the part of brain systems subserving spatial cognition, which we will describe next.

The Spatial Brain

Although it has long been agreed that spatial cognition is mediated by the brain, only in recent years have details of the brain mediation in spatial cognition become increasingly clear, thanks to advances in neuroscience, neuropathology, and brain imaging. One important detail concerns the increasing recognition that there exists multiple separated but interdependent brain systems that are especially crucial for spatial information processing and each of them adopts distinctive representational schema and thus holds different views of space (e.g., Burgess, Jeffery, & O'Keefe, 1999; see Figure 1).

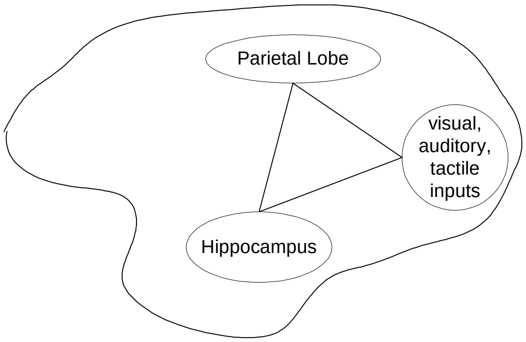

Figure 1. Homunculus of the spatial brain.

One such "space center" is the parietal cortex. It has long been believed that the parietal cortex, particularly the posterior parietal cortex, is one of the major neural substrates underlying important spatial functions in humans and lower primates. Neuroanatomically, the posterior parietal cortex is part of the dorsal "where" pathway. It receives projections from multiple sensory modalities, including visual, somatasensory, and auditory. In addition, it receives inputs from the subcortical collicular pathway, which consists of the superior colliculus and the pulvinar and is thought to be closely related to spatial orienting and eye movement control. Taken together, this pattern of cortical connections makes the posterior parietal cortex an ideal system for extracting and integrating spatial information from multiple modality-specific and unstable sensory channels and achieving supramodal and more stable spatial representations.

The most compelling support for this conception comes from the so-called hemispatial neglect. Hemispatial neglect is a fairly common neuropsychological impairment following unilateral (inferior) posterior parietal damage, especially in the right hemisphere. In typical cases patients neglect people, objects, and events in the contralateral hemispace. Obviously, these patients lost their ability to process information about this side of space. Being blind, deaf, and numb on this side of space, they feel that the contralesional space simply does *not* exist (Farah, 2000).

Hemispatial neglect can be further classified. Depending upon the area of damage in the parietal cortex, patients may neglect only one side of their body (e.g., unable to find one's left arm), neglect only near space (within arm's reach) but not far space or vice versa, show motor neglect (e.g., unable to move the contralesional side of the body), or show premotor neglect (e.g., unable to launch actions into the affect side of space). See Farah (2000) for a more complete treatment of hemispatial neglect.

These seemingly intriguing neglect patterns illustrate two important properties of the parietal cortex as a spatial information processing center. First, spatial representations in the parietal cortex are generally egocentric, which means that the frames of reference (FORs) it uses to represent space are centered on body parts. Egocentric FORs are in contrast to allocentric FORs, which are fixed to the environment itself or to individual objects in the environment. Coding space in egocentric FORs suffer poor stability in that body movements invalidate spatial representations. However, egocentric FOR-based representations afford fast actions – information for moving eyes to fixate, turning head to face, moving arms to reach, and moving body to translate is readily available, which makes much evolutionary sense. Second, there exist multiple egocentric FOR-based representations in the parietal cortex. In a certain sense the parietal cortex is both a unified and modular space center in the brain. It is unified in that it is supramodal – spatial information from multiple sensory modalities is co-registered and integrated here. It is modular in that this supramodal spatial information is then quickly and automatically transformed into multiple effector (eye, head, arm, body)-centered frameworks for guiding behavior. Consequently, the seemingly unified physical space is no longer unified but becomes segmented in the parietal cortex. Space is segmented based on the possible effectors to allow rapid reactions. The arm-reachable space is the only space meaningful for the arm-centered representation in the parietal cortex; when the brain system responsible for this representation is damaged, that space no long exists.

The notion that multiple segmented spatial representations exist in the parietal cortex has gained further support recently in single unit recording studies (see Colby & Goldberg for a review, 1999). It has been shown that the intraparietal sulcus (IPs), which separates the superior from the inferior parietal cortex, consists of important subareas that underlie this multi-representational scheme. For example, evidence has shown that neurons in the ventral intraparietal area (VIP) contribute to the representation of perioral space (i.e., space near to the body surface); and neurons in the medial intraparietal area (MIP) contribute to the representation of immediate extrapersonal space (i.e., space within reach of arm). The lateral intraparietal area (LIP) is particularly interesting. It is generally agreed that its neurons represent the space that can be explored by eye movements (e.g., visible space). More detailed analyses show that LIP neurons can encode this space in either eye-centered FOR (for both overt and covert attentional shifting, see Corbetta et al, 1998; and even for visually guided reaching, see Snyder, 2000), or body-centered FOR (when the head is not fixed, see Snyder et al, 1998). A nearby parietal area, 7a, is shown to encode the space in which the whole organism can walk around in a world-fixed FOR, based mainly on vestibular signals (Snyder et al, 1998).

Another brain system that is related to spatial cognition is the hippocampus, a distinctive structure in the back of the temporal lobe. The hippocampus sits on the top of the cortical hierarchy, receiving inputs from various cortical areas that essentially represent the entire cortical state. Since the discovery of place cells – cells in the rat hippocampus that fire when the animal is in a particular location in its environment, regardless of what direction the animal is facing and regardless of what the animal is doing, the functions of the hippocampus and related cortical structures in spatial navigation and episodic memory have been extensively studied and debated (see O'Keefe & Nadel, 1978; Squire, 1992; Nadel & Eichenbaum, 1999). Despite the lack of complete consensus, it is broadly agreed that the hippocampal system plays important roles in processing and storing topographical spatial information, in both rodents and humans (e.g., Redish, 1999; Teng & Squire, 1999; Maguire et al, 1999; Best et al, 2001).

One particularly influential framework is the cognitive map theory (O'Keefe & Nadel, 1978). According to this theory, the hippocampus is central to the construction of a cognitive map that encodes a rat's environment in a holistic and allocentric way. Specifically, "spaceless data enter the hippocampal system and cognitive maps come out. The spatial relations among objects which are embodied in the map are constructed within the mapping system" (O'Keefe and Nadel, 1979, p520). The hippocampus, therefore, maintains a two-dimensional Cartesian representation of the animal's environment and the activation of each place cell represents the animal's presence at a particular set of coordinates within the representation. Recent evidence from functional brain imaging has shown strong parallels in the neural basis of navigation between humans and animals though the parahippocampal area may be more involved in humans (e.g., Aguirre et al, 1996; Maguire, 1997; Maguire et al, 1999).

In sum, although it is very likely that other brain systems (e.g., the frontal lobe) are also involved in human spatial information processing, at least two brain systems, the parietal cortex and the hippocampus, are found to be especially critical. They form two space centers in the brain, with each specialized for different types of representations. Consequently, it seems that space is represented in the mind not once but multiple times. While the parietal cortex segments and represents it in multiple egocentric FORs, the hippocampal system is central to the construction of a holistic and allocentric representation of space. Apparently both systems are important in order to perform spatial tasks. Efforts have been made recently to study how the two systems might interact and work together (e.g., Burgess, Jeffery, & O'Keefe, 1999).

Psychological Space as Maps of Salience

What does a psychological space look like, given a specific FOR? We can envision a physical space as a three-dimensional continuous field, which is filled with uncountable number of points with neighboring points being unlimitedly close to each other (indeed, whether a physical space (and time) is quantized is still an open question). Obviously, a psychological space is quite different. It does not contain uncountable number of locations, nor does it allow unlimited spatial resolutions. Recent evidence from single unit recordings and brain imaging sheds important light on what is represented in a psychological space.

Gottlieb and colleagues (1998) investigated the firing patterns of neurons in monkey's LIP. They found that neurons show strong responses to stimuli appearing abruptly in their receptive fields. However, these neurons show little or no response to stimuli brought into their receptive field by saccades, unless the stimuli were made behaviorally significant. The authors suggest that the entire visual space is only weakly represented, with the most salient or behaviorally relevant objects being strongly represented.

It is important to note that a spatial location can become salient, or behaviorally significant, without being occupied by an object. A location where an interesting object is going to appear or has appeared before can be salient and needs to be represented. Corbetta et al (2000), using normal subjects and event-related functional magnetic resonance, show that the IPs becomes active as soon as a location is made relevant (salient) and attended before the presentation of stimuli. Similarly, Duhamel et al (1992) asked their patient, who suffered right frontoparietal damage, to visually track a sequence of quickly appearing-then-disappearing targets. The patient's systematic failure in this simple task indicated that she could not maintain an updated (salience) map induced by previously-presented stimuli.

These findings lead us to speculate that a psychological space, instead of a genuine copy of it corresponding physical space, is a map of salience. In such a map, only a few salient locations, defined by behavioral significance, are strongly represented, and all other locations are only weakly represented or "do not exist". To specify the relations among salient locations (e.g., distance) in a map, the measuring unit has to be defined. This unit, termed spatial JND (just noticeable difference), is map-specific and determined by, among other factors, the involving locations' salience measures and the base FOR. Therefore, the measuring unit in an arm-based FOR is different from that in an eye-based FOR. In addition, the distance from a more salient location to a less salient location may be measured differently from that in the opposite direction, indicating an asymmetry. In such a fashion, it seems that a psychological space can be quantized, based on the concepts of salience and spatial JND.

Summary in FORMS

We end this paper by summarizing the above-reviewed findings and speculations in the framework of FORMS (FOR-based Map of Salience), a theory about how the brain and the mind understand space.

Spatial cognition is a basic brain function with the distinct computational goal: to understand space by identifying and emphasizing important object-to-self and object-to-object spatial relations. While the physical space can be envisioned as a unified and continuous field, there is no such single unified psychological space. Space is represented in the brain and in the mind not once but multiple times, not unified but segmented. Each representation is a salience map with a distinctive FOR.

At a broad level, there exist at least two space centers in the brain. While the posterior parietal cortex subserves egocentric spatial representations, which are necessary for fast reacting, the hippocampal formation subserves allocentric spatial representations, which are more stable and are useful for topographical information processing and long-term storage. At a finer grained level, a psychological space is often supramodal but intention- or action-specific.

A psychological space is not a detailed map about arbitrary objects or arbitrary locations. It is a map of a set of salient locations and their relations. A spatial location becomes salient and gets to be registered in a salience map not because it is occupied by an object, but because it is behaviorally significant. This can occur under multiple conditions, including a) an interesting object appears in that position; b) an interesting object is to appear in that position (prediction); and c) an interesting object appeared in that position some time ago (memory). The concept of spatial JND provides further details on how to measure the relations among salient locations.

It is believed that FORMS enjoys solid neuroscience evidence support and is consistent with many behavioral findings. Further effort is clearly needed to computationally implement and evaluate it.

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References

Aguirre, G. K., Detre, J. A., Alsop, D. C., & D'Esposito, M. (1996). The parahippocampus subserves topographical learning in man. *Cerebral Cortex, 6,* 823-829.

Best, P. J., White, A. M., & Minai, A. (2001). Spatial processing in the brain: The activity of hippocampal place cells. *Annual Review of Neuroscience, 24,* 459-486.

Burgess, N., Jeffery, K. J., & O'Keefe, J. (1999). *The hippocamal and parietal foundations of spatial cognition.* New York: Oxford University Press.

Colby, C. L., Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience, 22,* 319-349.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Steven, E. P., Raichle, M. E., Van Essen, D. C., Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21,* 761-773.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience, 3,* 292-297.

Fan, J., MaCandliss, B. D., Sommer, T., Raz, A., & Posner, M. I. (in press). Testing the efficiency and independence of attentional networks. *Journal of Cognitive Neuroscience.*

Farah, M. J. (2000). *The cognitive neuroscience of vision.* Malden, MA: Blackwell Publishers.

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature, 391,* 481-484.

Hunt, E. & Waller, D. (1999). Orientation and wayfinding: A review. *ONR Technical Report N00014-96-0380*. Arlington, VA: Office of Naval Research.

Maguire, E. A. (1999). Hippocampal involvement in human topographical memory: Evidence from functional imaging. *Philosophical Transactions Royal Society London B, 352,* 1475-1480.

Maguire, E. A., Burgess, N., & O'Keefe. (1999). Human spatial navigation: Cognitive maps, sexual dimorphism, and neural substrates. *Current Opinion in Neurobiology, 9,* 171-177.

Marr, D. (1982). *Vision.* San Francisco, CA: Freeman.

McDonald, T. P. & Pellegrino, J. W. (1993). Psychological perspectives on spatial cognition. In T. Garling and R.G. Golledge (Eds.) *Behavior and Environment: Psychological and Geographic Perspectives.* N. Holland: Elsevier.

Nadel, L., & Eichenbaum, H. (1999). Introduction to the special issue on place cells. *Hippocampus, 9,* 341-345.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* New York: Oxford University Press.

O'Keefe, J., & Nadel, L. (1979). Precis of O'Keefe and Nadel's The hippocampus as a cognitive map, and Author's Response to Commentaries. *Behavioral Brain Science, 2,* 487-534.

Posner, M. I. & Petersen, S. E. (1990). The attention systems of the human brain. *Annual Review of Neuroscience, 13,* 25-42.

Redish, A. D. (1999). *Beyond the cognitive map: From place cells to episodic memory.* Cambridge, MA: MIT Press.

Snyder, L. H. (2000). Coordinate transformations for eye and arm movements in the brain. *Current Opinion in Neurobiology, 10,* 747-754.

Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature, 394,* 887-891.

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review, 99,* 195-231.

Teng, E., & Squire, L. R. (1999). Memory for palces learned long ago is intact after hippocampal damage. *Nature, 400,* 675-677.

Tversky, B. (2000). Remembering Spaces. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford Handbook of Memory.* New York: Oxford University Press.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A.Goodale, and R. J. W. Mansfield (eds), *Analysis of Visual Behavior.* Cambridge, MA: MIT Press.