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Quick guide

Cognitive maps

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What is a cognitive map? The term ‘cognitive map’ was introduced by the psychologist Edward C. Tolman in his 1948 paper *Cognitive Maps in Rats and Men.* In this synthesis of much of his earlier work, Tolman argued that animals form internal representations of spatial relationships, rather than relying solely on simple stimulus–response associations. Tolman did not provide a strict formal definition of the concept. At a time when behaviorism dominated psychology, even proposing the existence of internal spatial representations was a radical idea. Instead of defining the cognitive map precisely, Tolman characterized it by the behaviors it enables. In particular, he suggested that animals possessing such representations should be able to take novel shortcuts and detour around blocked paths. Thus, the existence of a cognitive map was inferred from behaviors indicating that animals could flexibly use a representation of their environment.

In his book *The Organization of Learning*, Charles R. Gallistel discussed cognitive maps as an example of how the brain encodes structured information about the world. Like Tolman, Gallistel did not offer a strict definition of the term, but he described the computational abilities that such a representation must support. Specifically, he argued that a cognitive map is an explicit internal metric representation of spatial relations among objects, enabling the computation of distances, directions, and novel routes. He further proposed that such maps should allow animals to perform vector computations, enabling them to infer the direction and distance to a goal after each movement.

What is the difference between a metric map and a sloppy graph? Although some evidence supports the existence of a metric cognitive map, consistent with a Euclidean representation of space, not everyone accepts the view that cognitive maps necessarily provide a metric representation. An alternative hypothesis suggests that the brain stores a topological, non-metric (graph-like) representation of space. Proponents of this view often cite systematic errors in human spatial judgments as evidence supporting this hypothesis — for example, consistent errors in estimates of distance, direction, and alignment. According to the graph hypothesis, spatial knowledge is organized more like a network: familiar places correspond to nodes, and connections between them correspond to graph-edges whose properties may depend on factors such as scale, familiarity, or travel cost. In such representations, spatial relationships may be approximately metric at a local scale but become distorted globally. They can also vary with context or experience. Nevertheless, even a graph-like representation could to some extent support behaviors such as detouring and shortcutting. This is because paths through the network can be recombined to generate novel routes, but they cannot guarantee usage of the most efficient shortcuts.

In light of this debate, a useful working definition of a cognitive spatial map (including both metric and topological maps) is an internal representation that encodes the spatial relationships among locations in a manner that supports flexible navigation. The ability to generate shortcuts or otherwise traverse novel trajectories is therefore a key behavioral signature of a cognitive map. Importantly, such maps need not depend on a single sensory modality: they may be constructed from any source of spatial information, including vision, audition, olfaction, or geomagnetic cues. Likewise, the underlying representations may be learned — as in visually acquired maps of familiar environments — or innate, as suggested for certain large-scale navigational systems such as magnetic maps.

How are cognitive maps studied? Cognitive maps have been studied extensively in laboratory settings. Tolman himself made one of the earliest experimental contributions. In a classic study, rats were trained to follow a route with several turns to reach a food reward. During testing, the familiar route was blocked and the animals were offered several alternative paths arranged in a fan spanning roughly 180° (aka the ‘sunburst maze’). Rather than choosing the path that initially matched the previously learned route’s direction, the rats tended to select the path pointing toward the original goal location. This behavior suggested that the animals relied on a representation of the spatial relationship between their current position and the goal, rather than merely memorizing a sequence of turns.

A widely used paradigm for studying spatial representations in the laboratory is the Morris water maze. In this task, an animal must locate a submerged escape platform in a circular pool using distal cues in the surrounding environment. After learning, animals can reach the platform from many starting positions by swimming directly toward it, suggesting that they estimate their location relative to external landmarks. This behavior is often interpreted as evidence that the animal has formed a map-like representation of the environment rather than relying on a fixed route.

Although laboratory paradigms have been highly influential, they operate at spatial scales that are much smaller than those encountered by animals in nature. Even small terrestrial mammals such as rats can navigate over hundreds of meters or more in the wild. Consequently, laboratory experiments may not fully capture the complexity or scale of real-world navigation. Studying cognitive maps under natural conditions is challenging for many reasons. For example, when working with wild animals whose prior experience is unknown, it is difficult to determine whether an observed shortcut is genuinely novel, as required for demonstrating a cognitive map, or the result of earlier exploration. A second difficulty is ruling out the possibility that an individual is simply following a conspecific. Because tracking devices can typically be deployed on only a small fraction of a population, and for limited time spans, these issues are not trivial to resolve.

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One common strategy to address these problems is to conduct translocation experiments, in which animals are captured and released at locations outside their normal home range. If the animal subsequently returns to its home area, this suggests that it can navigate over unfamiliar terrain. In practice, this often requires moving the animals very large distances, sometimes hundreds or thousands of kilometers. However, such experiments are only suitable for species that possess large-scale or even global maps — for example those based on the Earth's magnetic field — because animals relying on small-to-medium scale maps derived from local sensory cues (such as vision) would not necessarily be expected to return from such distant locations. An alternative approach developed in our lab is to establish an open colony (of bats in our case) where animals are free to leave. This setup allows studying the same individual continuously over very long time periods and to track its full history in some cases.

A complementary method for studying cognitive maps is the use of virtual reality (VR) environments. VR allows researchers to simulate large spatial environments while precisely controlling sensory cues and recording behavior or neural activity at high resolution. In animals, VR has mostly been used to study navigation in insects and rodents, often with the animal tethered in flight or while walking on a spherical or linear treadmill. Such setups have been particularly useful for investigating the neural basis of spatial coding. With human subjects, VR experiments make it possible to manipulate routes and landmarks easily, allowing researchers to probe spatial representations and decision making. However, many human VR studies are conducted in stationary setups, by using a joystick, which lack the full sensorimotor feedback associated with natural movement and thus might not accurately represent real-life navigation.

How are cognitive maps encoded in the brain? In *The Hippocampus as a Cognitive Map*, O'Keefe and Nadel proposed that the hippocampus functions as a spatial mapping system that forms an internal representation — or cognitive map — of the environment. This idea was motivated by the earlier discovery of 'place cells' in the hippocampus, neurons that fire when an animal occupies a specific location in space. Place cells were first identified in rodents and have since been observed in many vertebrates, including in freely flying bats where they are thought to represent three-dimensional position. Based on these neural findings, O'Keefe and Nadel argued that cognitive maps are allocentric — that is, world-centered rather than body-centered — and metrically encode spatial relationships between locations.

Subsequent discoveries greatly expanded our understanding of how the brain represents space, although how this representation facilitates actual navigation is still debated. Among the most influential findings were those of 'grid cells' in the entorhinal cortex, which fire in a periodic lattice-like pattern and are thought to contribute to estimating distance and position, and 'head-direction' cells, which track the animal's allocentric orientation in space and may function as a neural compass. Other studies have also found egocentric representations of space in the brain, including neural coding of direction and distance to navigational goals. More recently, studies using functional MRI have extended these insights to humans, providing evidence that the hippocampus and surrounding medial temporal lobe structures support map-like representations of space during navigation similar to what was found in rodents.

Are there non-spatial cognitive maps? Substantial evidence suggests that the same neural circuits in the hippocampus and entorhinal cortex that encode spatial relationships can also form internal representations of non-spatial relationships among objects, events, and concepts. For example, neural activity in the hippocampal–entorhinal system has been shown to represent relationships in acoustic dimensions, such as pitch space, as well as conceptual and social relationships. These findings support the idea that spatial neural representations may generalize beyond physical space to encode abstract relational structures. From an evolutionary perspective, one interesting hypothesis proposes that spatial navigation was the first domain in which relational mapping evolved, given its fundamental importance for survival and its map-like natural structure. The neural mechanisms originally supporting spatial maps may then have been co-opted to represent relationships in other cognitive domains. If this hypothesis is correct, it suggests that the way many concepts are represented in the brain may be strongly shaped by the structure and properties of physical space.

Where can I find out more?

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DECLARATION OF INTERESTS

The author declares no competing interests.

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