# The Neuropsychology of Spatial Cognition in the Rat

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**ABSTRACT:** This article provides a review of the neural mechanisms of spatial cognition in the rat. A survey of the literature shows that the rat has spatial capabilities that can be explained only if one assumes that it possesses a representation of some features of the environment. The scope of such a representation may, however, be more limited than what is implied by the hypothesis of a bird's-eye view of the environment. The best documented spatial ability of the rat is illustrated by its efficiency in performing the water maze navigation task. A review of recent neurobiological data collected while a rat was performing this task suggests that several brain structures make unique contributions to spatial navigation. In particular, the hippocampal formation and the associative (posterior) parietal cortex seem to handle different aspects of navigation and to be differentially involved in the various stages of spatial memory formation. Electrophysiological data support the hypothesis that the hippocampal formation is concerned with rapidly building associative memories of spatial relationships within the environment. In contrast, the associative parietal cortex might be involved in more abstract spatial processing, resulting in a metric representation of spatial information collected during movements.

**KEY WORDS:** spatial navigation, hippocampal formation, parietal cortex, place and head direction cells, neural mechanisms.

## I. INTRODUCTION

Recent years have witnessed a growing interest in the ability of the rat to form spatial representations of its environment.[1-3] One reason for this interest lies in the impressive capabilities of the rat to compute optimal paths through space. These capabilities appear to require sophisticated processes that allow the integration and manipulation of spatial information about the environment. As will become evident later in this review, the exact nature of the spatial representations involved in such processes is still a matter of debate. Another reason for this interest is the discovery, more than two decades ago, of a strong relationship between the activity of specific neurons in the rat brain and the location of the animal.[4] The combination of these two aspects has caused a great deal of research, resulting in a number of tentative possibilities for integrating complex spatial capabilities in various neural circuits.[5-8] Nevertheless, issues remain that represent a real challenge if we are to understand exactly how the brain creates solutions to navigation problems. The aims of this paper are to provide a review of the behavioral and neural aspects of the rat spatial cognition and to identify some issues that should be addressed to work out a general explanatory model.

## II. WHAT IS SPATIAL COGNITION?

### A. Statement of the Problem

This section briefly examines the mechanisms likely to guide spatial behavior, and thus it stresses the main concerns of the review. When a rat moves toward a goal location, it may do so very simply by being directed by a particular cue or a stimulus gradient directly associated with the goal, by performing a previously learned motor routine, or by some combination of these two el-

ementary mechanisms. Though they may be efficient in a number of situations, these mechanisms do not require a spatial representation of the environment and do not, therefore, put any burden on a spatial information-processing system. Accordingly, such behaviors are not further addressed in the following sections. Rather, the focus is on how spatial information from the environment is acquired and used by the animal so as to allow the emergence of flexible spatial behavior.[9]

Behavioral experiments clearly show that rats can perform efficient navigation based on mechanisms that do not involve the use of goal-associated beacons or of fixed routes previously learned. Under these conditions, navigation requires at least a representation of the goal location, and possibly of some features of the spatial layout. Such a spatial representation maintains a record of spatial facts about the environment. This record is used to generate paths that, although constrained by the structure of the environment, are not specified by the representation itself.[10]

Spatial representations are usually referred to as cognitive maps, that is, internal models of the external environment in which acquired spatial information can be internally reorganized.[11] In fact, the term *cognitive map* has been used in different contexts and with different meanings, so that its scope is often difficult to determine. For clarification, we distinguish three levels of spatial representation, presumably of increasing complexity. In the lowest level, only a single location acting as a goal is either egocentrically or exocentrically represented (such low-level spatial representations, requiring only a limited amount of spatial knowledge, are briefly addressed in the next section).

In the second, intermediate level, many places (not restricted to goals) and some of their relationships are represented with respect to the environment. Although the coding of these places is not assumed to depend on their status, the most visited places are likely to be represented in fine detail. This type of spatial representation requires a considerably greater amount of spatial knowledge and is the main focus of this review.

Finally, spatial representations of the most sophisticated type are map-like representations of the whole environment (survey maps). In principle, survey maps allow remote portions of space to be represented and novel, optimal routes to be generated even when there is no overlap in the perception of the landmarks available at the origin and goal of the path. However, since there is no evidence that mammals (with the exception of humans) are able to build survey maps of their environment, these highest level spatial representations are not addressed further.

## B. Egocentric Versus Exocentric Coding

The first issue that must be addressed to account for the rat's ability to generate an optimal path toward a goal on the basis of an internal representation concerns the mode of information coding. At this point, two very different processes must be dissociated (such a dissociation does not preclude that the two processes may share some information; see section VI.B). The goal location can be memorized in the form of an egocentric coding (i.e., self-referred), enabling the animal to perform vector (route-based) navigation, or in the form of an exocentric coding (i.e., referred to an external frame of reference provided by the environment), enabling the animal to perform place (location-based) navigation. These two coding processes have been demonstrated in mammals, birds, and insects.[12]

The egocentric coding process involves a path integration (or dead reckoning) mechanism that enables the animal to continuously update the vector that specifies the head-referred bearing and the distance to the memorized goal location on the basis of information collected en route about its own translations (i.e., straight movements) and rotations (i.e., changes of direction).[13] This process has the major advantages that information to be stored is limited to two parameters and that no prior exploration of the environment is required to ensure correct navigation to the goal. Its major drawback is that the computation of the two parameters is subject to cumulative error notably in the estimate of rotations.[14] This problem is particularly acute in mammals.[15] Indeed, since there is no compelling evidence that mammals can use the sun or a magnetic compass as an external reference direction, rotations can be measured only on the basis of internal motion-related signals (e.g., vestibular inputs), causing errors to accumulate very quickly.[14] A possible solution to this problem involves the recalibration of ro-

tation information on the basis of visual (or other sensory) information from the environment.[16] However, this recalibration proves efficient only if the landmarks are very remote (e.g., mountain peaks), so that they can serve as a compass. Closer landmarks are subject to motion parallax during the animal's translations. Because most animals move by combining translations and rotations, the apparent rotation of landmarks is not a valid means of calibrating the amount of rotation actually performed, unless the exact distance to the landmarks is well known. Since it requires no storage of information about the spatial features of the environment, the egocentric coding process is unlikely to be adequate for the study of spatial cognition.

In contrast, the exocentric coding process involves the gathering and storage of spatial information about the environment. The amount of spatial information that is stored is not necessarily very large. For instance, a low-level exocentric representation involves the memory of a single goal location in the form of a snapshot that specifies the apparent configuration of surrounding landmarks as they are perceived from the goal location. This representation is sufficient to enable a bee to navigate efficiently by moving step by step so as to progressively reduce the discrepancy between its current view of the landmarks and its memorized snapshot.[17-19] Much as in the egocentric representation, the navigational process afforded by this type of exocentric representation does not require prior exploration of the environment, but it remains rigid.

Another, higher level, form of exocentric coding involves the ability of the rat to build up representations of places independent of their status (an ability usually referred to as latent learning), and representations of the spatial relationships between these places. Stated in these terms, it becomes evident that the exocentric coding process has the major advantage of making the navigational process much more flexible than the simple snapshot coding system. Its major drawback, however, is that it requires the storage of a large amount of information about the environment. As a result, such representations are operational only once most of the environment has been explored. Evolutionary pressure may have shaped specialized memory systems that deal adequately with the task of storing large amounts

of information.[20] It is likely that this higher level type of exocentric spatial memory in mammals is a good example of such a memory system.

## III. EVIDENCE FOR SPATIAL COGNITION

### A. Place Navigation

The most compelling evidence for the notion that a rat stores spatial information about its environment and uses this knowledge to find direct paths stems from the observation of its orientation behavior in open areas. An illustration of this process is provided by the rats' ability to navigate efficiently in the water maze task.[21] In this task, a swimming rat can escape from water by finding a safe platform in a pool filled with opaque water. As the starting position of the rat is changed from trial to trial and the platform is located beneath the surface of the water, the rat must rely on the array of visual cues located outside the swimming pool so as to infer the platform location. Analyses of the paths (e.g., length, directionality, search distribution[22]) taken to reach the platform show that, after a few training trials, the rat swims almost directly toward the platform. Once trained in the basic task, the rat can quickly learn new goal locations each day.[23] Even more importantly, it shows immediate transfer when novel start points to a familiar goal are used. To do so, however, the rat must have previously had unrestricted access to all parts of the pool.[24,25] When rats are physically prevented from swimming in one half of the pool during training, subsequent testing for navigation from the restricted part results in inaccurate performance. These experiments support the importance of exploration in the formation of spatial representations.[26-28]

The straightness of swimming paths displayed by the rat when it is started from different locations in the water maze indicates that it is not just trying to continually adjust its current position in reference to a memorized snapshot taken at the goal. Such a solution, which relies on step-by-step movements, would result in more erratic movements. Instead, the rat seems to have some knowledge of the distance and direction of its final destination, beginning at the start location, and sets its course immediately, so as to reach the goal as soon as possible. Proof that mammals are

able to plan their course based on information available at the start was provided by experiments using gerbils.[29] These animals were trained to move toward a hidden food source that could be located relative to three distant landmarks. Once an animal had learned to navigate to the goal location in a lit condition, it was tested with the lights turned off immediately after it began to move toward the target. The fact that gerbils' performance was not disrupted by the sudden darkness suggests that their course had been planned at the start of the trial. Note, however, that more or less efficient navigation has been accounted for recently by several associative models.[5,30,31] Nevertheless, the model with the strongest S-R flavor (and no planning ability)[30] does not result in a navigation performance as efficient as that observed in rats.

## B. Shortcutting and Detour Behavior

The ability to generate a plan suggests the existence of a stored representation of the spatial relationship between the goal and current position of the animal in the environment. Such a representation allows an animal to take shortcuts and detours. The prototypic detour situation consists of blocking a route previously used to reach a baited goal, thus requiring an animal to reorganize its path under these altered circumstances.[32,33] It is generally observed that animals quickly select the next most appropriate path leading to the goal.[34] Since one function of spatial representations concerns the ability of an animal to store in memory important places and to navigate efficiently to these places, animals should be aware of the structural properties of paths. Although this issue is difficult to address empirically, there is evidence that rats pay attention to such properties and that their spatial knowledge does not amount simply to a representation of the goal location. For instance, it has been found that, under some circumstances, rats select specific routes that result in a reduction in complexity of the problem.[35] Additional support for the notion that animals pay attention to the structural properties of space comes from studies on cats in which the choice of a path was shown to be influenced by its length and directionality.[36] Thus, spatial knowledge is not lim-

ited to representations of start and goal locations but also encompasses some knowledge of the structure of the environment. Note that this observation can be made only if the goal is hidden. A visible goal acts as an anchor that shifts control over behavior from spatially based information to sensory guidance. A visible goal caused cats not to make optimal choices about path length. Instead, cats tended to take the path that most closely approximated the goal direction from the start. Although no equivalent data are available from the rat, it is likely that similar processes are in order.

## C. Memory of Multiple Goals

Rats perform very well on many spatial working memory tasks. This fact suggests the existence of a flexible memory system for storing multiple locations. This demonstration relies on the use of a task in which a rat is required to gather food at the end of the eight arms of an elevated radial maze.[37] Since arms depleted of food are not rebaited, the rat learns to avoid locations that have already been visited. It has been demonstrated that a rat generally does not rely on algorithmic responding (e.g., visiting adjacent arms from one choice to another) or local information (such as scent trails deposited during previous visits), but rather forms a memory of depleted arms.[38] What must be remembered during a trial are the behavioral events associated with entering each arm.[39] To be useful, the encoding of such events must be associated with perceptually defined maze arms. This association requires some form of spatial discrimination, for each arm is defined most easily by its location. Evidence suggests that the memory of depleted arms is based on an exocentric representation of the food locations updated following each choice, and not based on a list of items.[40] Arguably, such representations store information about the position of each arm relative to the configuration of visual cues within the testing room.[41-43] Although there is still some controversy about the exact nature of the memory processes involved in the radial maze task,[41,44,45] it is clear that performance relies on an adaptive spatial memory system that allows for flexible responding. This memory system is useful in a number of situations including those involving several food source locations in an open field.[46]

## D. Detection of Spatial Changes

One prediction of the hypothesis that a rat represents some features of the spatial layout is that it should be able to detect spatial changes in the environment. Several studies have shown that rodents can detect such changes. In general, changing the configuration of objects in a previously explored arena induces a renewal of exploratory activity aimed at displaced objects.[47–51] In a series of experiments using hamsters, exploratory behavior was examined as a function of the type of change brought about by the displacement of objects.[47,48] The general conclusions from these studies were that the animal keeps a record of the spatial situation and that this record is specific to certain classes of spatial relationships. Changes that induce the greatest reaction are those that affect either the overall geometrical arrangement of the object set or the topological relationships among the objects. In contrast, changes that affect only the metric relationships (i.e., distances) between the objects do not appear to induce a significant renewal of exploration, suggesting that the overall configuration is privileged over the absolute position of objects.

## IV. NATURE OF THE RAT SPATIAL REPRESENTATION: WHAT IS STORED?

### A. Geometry and Landmarks

Recognizing that animals are able to use representations of their spatial environment does not say a lot about the nature of such representations. Evidence cited in previous sections shows that these representations might not encompass all aspects of the environment. While it is clear that a rat's representation stores information about configurations of cues, there has been some debate about what constitutes an appropriate spatial cue. For example, several authors have emphasized the importance of information provided by the "geometrical shape" of the environment.[1,10,52] Support for this assumption is based on the observation that, when a rat is required to orient in a rectangular chamber, it mainly relies on the shape of the chamber and neglects potential cues provided by either discrete inserts placed at corners or sa-lient visual patterns placed on walls. It is somewhat surprising to note that a recent study revealed that a similar hierarchy of spatial cues seems to be operating in young children who primarily base their orientations on the geometrical shape of a large rectangular room.[53]

The preponderance of the overall geometrical shape should not, however, obscure the fact that the rat also stores information about configurations of discrete cues. For instance, the rearrangement of extramaze visual cues in an otherwise homogeneous (cue-controlled) environment markedly affects the behavior of rats performing the radial maze task.[42] Also, rats are able to integrate the intramaze stimuli in a representation used to guide goal-directed behavior.[54] Finally, exploration experiments reveal that rodents form a representation of the configuration of small intramaze objects.[47,48,50] Recent studies on mice[55] and birds[56,57] suggest, however, that such objects, although clearly noticed, are not so useful for place navigation. Therefore, animals would filter out high spatial frequencies provided by fine-grain cues (such as small objects) and rely only on coarse-grain cues in exocentric localization. Eventually, only those cues that outline the geometrical shape of the environment would act as "true" landmarks. As a result, there would be no real gap between the concepts of geometry and landmarks. The filtering function might have emerged under evolutionnary pressure because of a twofold advantage: (1) it eliminates cues that are not reliable in exocentric localization; (2) it dramatically reduces the cognitive burden that bears on the exocentric localization system.

In addition to the general characteristics of space that allow unique locations to be identified in the environment, the rats are aware of certain of its structural properties such as the routes that link privileged locations. Thus, as shown in section III.B, choice of routes is markedly affected by their structural (e.g., length and directionality) and local properties (e.g., presence of choice points, degree of incline).[35,58–60]

### B. Topology and Metrics

Together, these studies make it clear that rats possess a representation of the geometry of their

environment. The representation is not, however, total: only certain spatial relationships are handled while others are not. Also, the representation is not homogeneous in that animals process certain locations in a more detailed way during exploration. This is not very surprising because space is not homogeneous. It is more surprising, however, that the topological relationships among such locations often have stronger control over spatial behavior than metric relationships do (see section III.D). In any case, it seems that the concept of a single overall spatial representation of the environment should be rejected. Instead, it appears that animals represent several distinct aspects of the environment. Recently, one of us hypothetized that such representations can be both topological, therefore affording relatively unstructured information about the connectivity within space (for example, place A is directly connected to place B but not to place C), and metric (for example, place A is a certain distance and direction from place B), affording more detailed information about specific relationships among places.[3] An additional idea was that topological information may be more rapidly acquired than metric information because metric encoding would largely rely on motion-related signals provided by repeated movements between places.[3] Although there is little direct empirical support for a dissociation between topological and metric information in the rat's spatial representation, the conception of a dual network has several major advantages over single-format conceptions[1,61,62] such as that of a metric / global representation of the environment.

## C. A Possible Model for Place Navigation

Given the complex nature of the stored spatial information, it is difficult to imagine a process that allows the rat to easily compute efficient paths through space. In the past, several solutions have been proposed, ranging from those relying on purely topological mechanisms[63] to those relying on purely metric mechanisms.[62,64] We now briefly summarize an intermediate place navigation model we have recently developed.[31] In our model, the information about the immedi-ate environment is provided by the head-referred bearings and vertical angular sizes of landmarks (i.e., local views). This type of two-dimensional angular information can be easily determined from the animal's current location at the retinal level. Local views of various directions from a given place are assumed to be linked together to form a 360° panorama (defined independently of the animal's heading) that constitutes a kind of place representation.[3] A panorama therefore encompasses locally the geometry of the environment defined on the basis of the landmarks as perceived from any specific place.

During exploration, the animal is assumed to build up associations between the current panorama and the panoramas experienced at neighboring places, as well as associations between the current panorama and an overall reference direction provided primarily by vestibular and other kinesthetic inputs (see section VI.C). The first type of association allows the topology of the environment to be taken into account locally, while the second type allows the extraction of an absolute angular reference from the local environment. According to this model, the animal would be able, after continuous exploration of the environment, to determine its current position (location and orientation) with respect to the environment on the basis of any local view. During navigation, the direction of the goal from the current place is then estimated on the basis of the distribution of the discrepancies between the panoramas experienced from the neighboring places of the current place and the panorama memorized from the goal, with respect to the overall reference direction. This model mainly works step by step, based on continuing environmental feedback. Nevertheless, it is possible to directly derive the direction and distance to the goal, even though the animal can no longer see the landmarks, because both the local topology embodied into the panorama associations and the associated overall reference direction provide enough information to thoroughly plan the course to the goal location from the start location. This model allows for better navigation performance than pure topological models and is more biologically plausible than pure metric models. In particular, it accounts for poor navigation performance when thorough exploration of the entire environment is impeded.[24–28]

## V. NEURAL MECHANISMS OF SPATIAL COGNITION

Since there is strong evidence that rats remember various aspects of their spatial environment, it seems natural to look for the brain processes that underlie this ability. This section provides a brief overview of the neural mechanisms of spatial cognition in the rat with an emphasis on the contribution of several brain structures. Although recent research has made significant contributions to our understanding of the brain, it is still a difficult task to understand how adaptive spatial behavior is generated with the brain. Part of this difficulty might lie in the crucial role assigned to the hippocampus. In spite of its importance, the hippocampus is certainly not the only area involved. As described below, other cortical structures are also critical in spatial functioning. Another reason for this difficulty may be that lesion or electrophysiological studies usually use confined situations as compared with behavioral work. The outcome is that the understanding of the neural mechanisms relies on a restricted view of spatial behavior. In that respect, the development of specific behavioral procedures such as the water maze navigation task[21] has made it possible to analyze in more detail the participation of several neural systems in various aspects of spatial processing.

### A. Dissociation Between Egocentric and Exocentric Information Processing

The first question that must be addressed is whether the brain is organized so that the two modes of spatial coding, namely, egocentric and exocentric, are dissociated. In other words, is there evidence for the specific involvement of brain systems in processing of spatial information relative to the subject and relative to the environment, respectively? The answer to this question is not so straightforward because it is difficult to disentangle the contribution of motion-related signals, which provide the basis for egocentric coding, to the exocentric processing of spatial information, which likely involves movements in space.[65] In spite of this difficulty, several studies have shown that the two systems may be distinct. Potegal was the first to propose that the caudate nucleus, which

is related to vestibular / proprioceptive functions, could act as an egocentric localization system.[66-68] Specifically, he demonstrated that caudate nucleus lesions in rats impair the performance of an egocentric localization task, while leaving unaffected the performance of an equally difficult task that did not require egocentric localization. Further work revealed that such lesions also disrupt performance of a "return from passive transport" task that could be solved only on the basis of vestibular information whereas hippocampal damage has little effect on the same task.[69,70]

Finally, the demonstration of functional dissociations between the effects of lesions of the dorsal striatum (which includes the caudate nucleus) and lesions of the hippocampus on spatial tasks that varied the involvement of egocentric and exocentric processing provided recent and independent confirmation that these two brain areas are involved in different systems that are concerned with the processing of information provided by the subject motor responses and with the processing of information about the environment, respectively.[71-77] An additional conclusion that stems from these studies is that, in spite of the necessary contribution of motion-related signals to exocentric processing, the ability of the rat to perform place navigation is relatively insensitive to manipulations that affect egocentric processing.

### B. Contribution of the Hippocampal Formation

As stated above, many accounts of hippocampal function have emphasized its role in spatial processing.[61,78,79] Although the hippocampus has been proposed to be involved in other functions,[39,80,81] there are at least two lines of evidence that support its primary involvement in spatial processing.

The first line of evidence comes from lesion studies showing that damage to the hippocampus and virtually all its associated structures (fornix, septum, entorhinal cortex, subiculum, postsubiculum) induces severe and permanent deficits in a wide variety of spatial abilities.[82] For example, rats with such lesions are impaired in the spatial version (with a hidden goal platform) of the water maze navigation task, but not

in its nonspatial version (goal platform visible or signaled by a salient beacon).[83-89] In addition, hippocampal rats have an impaired spatial memory in the radial maze.[38,90-92] Exploration is also strongly altered following damage to the hippocampal formation. In addition to their locomotor hyperactivity and abnormal pattern of habituation,[93-96] hippocampal rats have impaired reactions to spatial novelty in that they fail to detect discrete changes in the topographical arrangement of an environment[97-100] learned after the lesion, yet their sensory discriminative abilities are generally left intact.

Although hippocampal damage markedly affects acquisition of new spatial information, retention of well-learned spatial information is often spared. For instance, hippocampal rats are able to navigate to a goal location learned before the lesion was made while they are unable to learn a new goal location.[101-103] The sparing of place navigation performance is most evident when there is a substantial delay between training and surgery.[104,105] These results, which are best described as a temporally graded impairment of premorbid memory, suggest that the hippocampus is not the long-term store of spatial information,[106] nor is it necessary for the kinematic aspects of place navigation at later stages. In addition, some functional recovery of place navigation ability is often observed. While hippocampal rats are consistently found to be impaired relative to control rats, their performance nevertheless may improve over time, resulting in a bias toward the goal location after extensive training.[86,89] However, such recovery is observed only when lesions are restricted to a specific portion of the hippocampal formation. In contrast, it is not observed with larger lesions, including portions of the entorhinal cortex and subiculum.[107] This suggests that the different components of the hippocampal formation make distinct contributions to place navigation, a conclusion further supported by the observation of distinctive swimming patterns following each type of lesion.[86,87,89]

The second and most crucial line of evidence in favor of the spatial function of the hippocampal formation is the existence of cells that carry a spatial signal. For practical reasons, cell activity is most commonly recorded in a "pellet-chasing" task that requires the animal to move constantly in a walled arena. This task differs markedly from the water maze navigation task in several respects such as motivation (appetitive vs. aversive), task requirements (no place has a specific valence vs. there is an explicit goal), and locomotion mode (walking vs. swimming). The assumption is that, even under these circumstances where there is no explicit goal, the animal *must* process spatial information. This procedure has the advantage that, if a cell is found that fires with respect to some aspect of space, the existence of this spatial signal cannot be accounted for by the learning of a specific behavior but is likely to reflect some genuine aspect of spatial processing.

Cells that carry a spatial signal are found in the hippocampus proper and closely related structures and can roughly be classified as place cells or head direction cells (however, finer distinctions can be drawn[5,108]). Place cells are hippocampal pyramidal cells whose firing is strongly correlated with the location of a freely moving rat in its environment.[4,109,110] Each place cell is characterized by a stable, spatially limited "firing field." The cell fires rapidly when the rat's head is inside its field and is usually silent elsewhere in the environment. Place cells show very similar properties whether the rat is engaged in a spatial learning task[111-115] or during spontaneous locomotion in an open field.[116-118] Although place cell firing may be modulated by nonspatial variables such as motion speed,[115] its most consistent correlate is the animal's specific location.[119] In general, place cells fire independently of head direction. For example, in closed walled arenas, place cell discharge is independent of the direction faced by the rat and varies only with location.[119] However, circumstances can be found under which place cells are both locationally and directionally selective. Usually the directional selectivity of place cells increases in apparatuses with well-defined pathways, such as in linear mazes or radial mazes.[112,120,121] As shown by neural network simulations, a possible explanation for increased directional selectivity of place cells in such apparatuses might lie in the mechanical constraints on the possible directions faced by the animal at specific locations.[122]

Hippocampal place cells have well-characterized properties. First, when rats are exposed to a new stimulus situation in an open field, place fields rapidly develop as the animal explores the

new environment.[123,124] Once established, the locations of firing fields are stationary and specific. Second, even though firing fields of hippocampal cells are controlled by the environment (e.g., rotating the cues around the open field induces a corresponding rotation of the firing field location), such a control is more complex than if caused by a mere sensory triggering. When controlled cues are removed, most place cells display firing fields remarkably similar to those observed when the cues were present. Such similarities concern the size of firing fields, their shape and their radial distance from the center of the apparatus, but not their angular location, which becomes unpredictable.[116] This property suggests that place cells encode information about locations in the environment rather than information about sensory views of the environment. Thus their firing is not triggered in a simple sensory fashion.[113,116] Only under specific circumstances, place cells can retain all aspects of their original characteristics in the absence of the controlling cues, including their actual location of firing in the environment. This occurs when the animal samples the environment just before the cues are removed, or the lights turned off. Under these conditions, motion-related signals are used by the hippocampal system to maintain the coherence of place cell firing.[113,123,125–128] Lastly, any change in the firing characteristics of a given cell is accompanied by a similar change in the firing characteristics of other simultaneously recorded cells. For instance, if the cues are rotated, the firing fields of all the cells will rotate the same extent and in the same direction. This is true both for predictable (i.e., under stimulus control) and unpredictable changes (e.g., when cues are removed). Therefore, place cells appear to form a tightly connected functional neural network.

Head direction cells are primarily found in the postsubiculum.[129–131] Recently, cells with similar properties have been found in the anterior[132] and lateral dorsal nuclei of the thalamus.[133] On anatomical grounds, all these regions have relatively direct connections with the hippocampus.[134,135] Although the firing patterns of head direction cells in all these areas depend on the heading of the animal, independently of its location, specific differences have also been reported. One such interesting difference is that anterior thalamic neurons shortly anticipate the future direction of the head whereas postsubicular neurons encode the current heading.[136,137] This suggests that the coding of head direction in the postsubiculum would result from cooperative activity in the anterior thalamus, this activity being mediated by angular head motion (mainly vestibular) signals.

Although much less studied, head direction cells share many properties with place cells, including being controlled by salient visual cues.[131] If such cues are rotated around the open field, the preferred direction of firing of head direction cells is rotated to an equal extent in the same direction. In addition, as place cells, head direction cells can maintain their activity when the environmental cues are removed, or the lights turned off, if the rat has had immediately prior exposure to the cues.[131] Head direction cell activity is therefore not simply visually triggered, as appears to be also the case of place cells. In the absence of visual information, motion-related signals are used to maintain coherent head direction cell activity. An additional observation is that, in the presence of conflicting motion-related signals, head direction cells primarily fire based on visual information.[138,139] Lastly, head direction cells do not function independently of each other. As revealed by simultaneous recordings, changes in activity of a given cell are accompanied by corresponding changes in activity of other cells, again suggesting the existence of a tightly connected functional neural network. Furthermore, a recent experiment in which place cells and head direction cells were simultaneously recorded revealed that the two classes of cells reacted in concert to the same manipulations of the environment.[140] The rotation of the locations of place cell firing fields was accompanied by a similar rotation of the preferred directions of firing of head direction cells. This result suggests that the two types of cells have access to the same information and function cooperatively to allow the rat to navigate efficiently by using consistent location and direction information about the relationship of the head position to the environment. However, the extent to which the coordinate systems of each class of cells would be permanently coupled in more complex environmental conditions is still an unsolved issue.

In addition to these two populations of cells, the hippocampal formation contains neurons whose spatial signals are more complex. For ex-

ample, cells from the medial entorhinal cortex,[141] dentate gyrus,[142] and subiculum[108,143] act like place cells although their firing fields are usually less specific and "noisier" than those of hippocampal place cells. Lastly, cells found in the subiculum have both location and direction correlates.[108] The resulting overall picture is that the hippocampus and related structures form a system where spatial information is processed and coherently organized. In summary, there is strong evidence that place and head direction cells are part of a widespread neural network concerned with the processing of spatial information. Although current evidence suggests that normal hippocampal function is required for place navigation, its exact role is still a matter for debate. In addition, it is not clear how the information processed in the hippocampus is passed onto other brain areas involved in spatial processing.

## C. Contribution of the Associative Parietal Cortex

Several recent studies have reported significant spatial deficits following damage to a number of neocortical areas. The most clear-cut deficits are found after lesions of the associative parietal cortex. On the basis of a study of its corticocortical and thalamocortical connections, Kolb and Walkey[144] have delineated a cortical area in the rat that is homologous to the primate posterior parietal cortex. Note, however, that other researchers have proposed a more anterior localization of the associative parietal cortex[145,146] with little overlapping between the two suggested loci. In spite of the difficulty caused by this difference in localization,[147,148] the general pattern of deficits produced by damage to each associative parietal cortex is consistent with its involvement in the exocentric processing of spatial information. Rats with such lesions are impaired in maze learning,[149–151] place navigation,[144,146,152–155] and spatial working memory,[144,154–156] while having no impairment in a visible goal platform water maze task.[144,157] In addition, damage to the associative parietal cortex does not usually result in any gross deficit in motor behavior[144,158] or simple sensory discriminations if the lesions do not extend too far into the posterior cortex.[147,159,160] Lastly, rats with associative parietal cortex dam-

age have impaired reactions to spatial novelty. Yet, their pattern of habituation as well as their reactions to nonspatial changes are unchanged relative to normal animals.[148,161]

Although rats with lesions of associative parietal cortex are impaired in place navigation, the magnitude of their deficit relative to that produced by hippocampal damage remains controversial. Whereas some studies report greater impairments after parietal damage than after hippocampal lesions,[146] the reverse pattern has also been reported.[144] It is likely that such variations can be accounted for by differences in localization and extent of lesions. These differences could also account for discrepant observations about the qualitative aspects of the spatial deficits in animals with damage to the associative parietal cortex. For instance, while rats with damage to the posterior region of the associative parietal cortex fail to detect the topographical rearrangement of a familiar arena, rats with damage to the anterior region seem to notice the change but fail to discriminate its exact locus.[148]

In spite of these inconsistencies, several major conclusions can be drawn. First, damage to the associative parietal cortex appears to affect both initial acquisition and retention of spatial information.[146] The paths of parietal rats are always variable, even with extended training.[144] In contrast, hippocampal rats tested for retention of spatial information that was well learned before surgery have spared spatial capabilities.[102–105,148,162] Thus, the involvement of parietal cortex and hippocampus appears to follow a distinct time course. The latter structure is useful early in the course of spatial learning while the former is useful in acquisition and performance of the place navigation task.[148,162]

Second, differences in the swimming patterns are observed in the rats with associative parietal cortex lesions and with hippocampal lesions when they are tested in the water maze task. While both lesions impair place navigation, only hippocampal animals are able to use a systematic strategy to reach the hidden platform (that is, they swim in circles at the appropriate distance from the pool wall[86]) whereas parietal animals display random swimming patterns.[146] This observation suggests that, although both groups are impaired, the nature of their impairment is different. There are several, certainly not exclusive, possible explana-

tions of the cause of the differences. The first is concerned with the format in which spatial information is processed by each structure. As assumed earlier, spatial representations can be both topological (i.e., coding for the connectivity of space) and metric (i.e., coding for distance and angular relations). The observed navigational patterns are not incompatible with the notion that these two categories of information could be separately processed by the hippocampus and the parietal cortex, respectively.[3,108,163] Following this idea, the acquisition of metric information would rely on motion-related signals during exploratory movements within the environment and therefore would proceed gradually.[3] Another related interpretation assumes that the associative parietal cortex would be involved in the computation of the fine adjustments of trajectories based on the spatial relationships between the landmarks. This interpretation is supported by single-unit studies showing that associative parietal cortical neurons have motion-related activity that can be strongly modulated by the animal's location in the radial maze.[7,164,165] This interpretation is not, however, well supported since clear-cut spatial deficits can be obtained in tasks that do not involve contingent reinforcement or the production of specific paths, such as in the exploration-reaction-to-change task,[148,161] following damage to the associative parietal cortex.

In summary, although there is a great deal of evidence for the involvement of the associative parietal cortex in spatial processing, its role remains controversial. The respective contributions of the associative parietal cortex and hippocampal formation to spatial cognition are not yet understood. The situation is complicated because other cortical areas have recently been shown from lesion and electrophysiological studies to be important in spatial processing. This is the case of the posterior cingulate (retrosplenial) cortex whose damage has been found to produce a severe spatial deficit in place navigation,[166] even though spatial memory does not seem to be affected.[167] In addition, neuronal firing in the retrosplenial cortex is often correlated with head direction.[168,169] Lastly, lesions of the medial frontal cortex result in spatial impairments.[170,171] However, frontal rats are not impaired in their behavioral reaction to topographical rearrangements.[98] There is some evidence that the frontal rats' spatial deficits can

be best explained as due to impaired working memory, precluding them from appropriately planning complex sequences of actions such as those required for accurate navigation.[172,173]

## VI. A FRAMEWORK FOR SPATIAL INFORMATION PROCESSING

### A. A Glance at Holistic Models

This review made it clear that both the hippocampal formation and associative parietal cortex have a key role in encoding and storing exocentric representations on the basis of egocentrically acquired information. This network of neural structures forms an integrated system important for spatial processing in which each component has its own specific role. In addition to lesion and electrophysiological evidence, the reciprocal anatomical connections among the hippocampal formation, the associative parietal cortex, and the retrosplenial cortex provide support for the contribution of these distinct brain areas to such a system. Although the current data make it difficult to draw definitive conclusions about their exact contributory role, general models that emphasize the existence of an integrated spatial information-processing system including the hippocampal formation and the associative parietal cortex are worth briefly mentioning here.

A very influential, previous model emphasized the possible role of the hippocampus acting as a device that would build an index of cortical addresses where memory engrams would be stored in long-term memory.[174] In this model, the cortical memory engram would be easily accessible via hippocampal addressing. However, "old" engrams could still be accessed in the absence of the hippocampus. In related models,[148,175] the hippocampus and associative parietal cortex are thought to respectively mediate new incoming information via a data-based spatial memory system and existing spatial knowledge via an expectancy-based spatial memory system. Although such models predict the pattern of spared and lost spatial abilities in acquisition and retention of place navigation following damage to hippocampal and neocortical sites, they fail to account for the qualitatively different navigational strategies observed after hippocampal and associative parietal corti-

cal lesions (section V.C). In contrast, a possible explanation of these different strategies considers the associative parietal cortex as an interface that would perform coordinate transformations allowing for integration of egocentrically collected information into an exocentric spatial reference framework[165] (a similar hypothesis has been proposed in humans[176]). Nevertheless, it is not clear how this model explains the different patterns of impairments in retention of spatial information learned before the lesion. Although the associative parietal cortex is certainly important for the transformation of egocentric to exocentric spatial information, it probably includes abstract processing of the transformed information. It could be involved in the storage of such information as well.

Another model, proposed by Poucet,[3] is that the hippocampus creates a topological representation that specifies the connectivity of space (that is, the neighborhood relationships between places), while the associative parietal cortex creates a metric representation largely based on information collected during movements in space. In this view, the hippocampus is required for the buildup of the spatial representation because of its central role in the processing of place and topological information, but its importance should decrease as the organism's experience with the environment increases. That hippocampal rats are able to navigate efficiently toward a goal well learned before the lesion[101,103–105] supports the idea that the hippocampus is critical in early stages of spatial information processing but not at later stages, and additionally suggests that it might not be essential for the kinematic (metric) aspects of navigation. These abilities would definitely be disrupted by damage to the associative parietal cortex. Because of its central role in concurrent representations of the movements and sensory environment and because of the reliance of such representations on exploration, the parietal cortex spatial representation would be necessary in both early and late stages of spatial processing. Although speculative, this model has the advantage that it fits the existing experimental data (see section V.C). In addition, it is supported by the existence of well-acknowledged anatomical connections between the hippocampus and the parietal cortex.[3] It is clear, however, that further work is required for explicitly testing some of the model's predictions, such as the experience-de-

pendent decreasing role of the hippocampus in place navigation. Furthermore, it will be important to establish whether the information that is permanently stored in the rat's spatial representation is primarily metric and is held by the associative parietal cortex. At this stage, it seems useful to look for a more specific conceptualization of how spatial information might be processed to provide the animal with spatial representations.

## B. Preliminary Remarks on the Flow of Information

The buildup of a spatial representation of the environment entails that sensory information, sequentially acquired as a result of the animal's movements, be integrated so as to allow the simultaneous access to relevant represented information. The sensory information consists of dynamic (route-based) and static (location-based) information. Dynamic information is provided by motion-related signals about translations (straight movements) and rotations (changes of direction) and stems mainly from the vestibular and proprioceptive/kinesthetic systems, and possibly from the visual flow. Static information about the environment (usually referred to as local views) is mainly visual but possibly involves both audition and olfaction as well. Efficient navigation requires that the goal location and the animal's current position be expressed with respect to the same frame of reference. Consequently, spatial information is differently processed in vector navigation and place navigation. Indeed, while both sensory inputs and motor outputs are necessarily defined egocentrically, the memory of the goal location is defined egocentrically in vector navigation and exocentrically in place navigation. Contrary to vector navigation, place navigation therefore requires spatial information to be processed through a "two-way converter" of frames of reference.[31]

In vector navigation, the egocentric coding of the goal location makes information processing straightforward. Only dynamic information is used. By means of a path integration mechanism that combines information about translations and rotations, the goal location is dynamically memorized as an updated egocentric coding that directly provides both the head-referred direction and distance to the goal. One neural system that is a good candidate as

the neuroanatomical locus for such dynamic information processing is the caudate nucleus.[67] The limitation of path integration is its high sensitivity to random noise generated during rotations. Hence, a rat can rely on vector navigation only when the initial path involves a few rotations. The advantage of vector navigation is that, contrary to place navigation, it does not require prior exploration of the environment. Thus, it can be used during initial exploration of a new environment to keep track egocentrically of some arbitrary points from which further investigation gradually proceeds.[177,178] In place navigation, both dynamic and static information are used,[16,31,179] and the exocentric coding of the goal location makes information processing more complex. In the remaining sections of this paper, we attempt to provide a tentative explanatory framework for the neural processes that underlie the exocentric coding process.

Before turning to this issue, however, a brief note of caution must be made. As a matter of fact, that dynamic information is used in both place and vector navigation has led some authors to stress that place navigation would rely on a dead reckoning or path integration process. This claim has resulted in some confusion in terminology. For clarity's sake, the terms *dead reckoning* and *path integration* should refer exclusively to the specific use of dynamic information in *vector navigation*, i.e., to the combination of rotation and translation information that enables the animal to update the relative location (with respect to the animal's position) of its starting point during its movements. Instead, these terms have been misleadingly employed to refer to various possible uses of dynamic information in *place navigation*. Thus, dead reckoning was used to refer to a simple heading monitoring involving only rotation information.[16] On the other hand, path integration was used to refer to the high-level representation of the path onto a survey map.[24] To our knowledge, such a path representation has been demontrated unambiguously only in humans.[180]

## C. Extracting Spatial Invariants in the Hippocampal Formation

Because of the lack of electrophysiological data, it is still a difficult task to assign a specific spatial function to the parietal cortex. In contrast, much more is known about the hippocampal formation, and many neural models have recently focused on its involvement in spatial processing. While it is beyond the scope of this article to detail these models (reviews can be found elsewhere[5,8,61,108,181]), we provide here a brief synthesis aimed at examining how the hippocampal formation can extract spatial invariants. In doing so, we refer only to the known properties of the two cell populations (i.e., place cells and head direction cells) found in the hippocampal formation. One such property we emphasize is that neither place cells nor head direction cells are simply sensorially triggered. Rather, they are part of a neural network that enables a rat to determine its current position (location and orientation) in the exocentric frame of reference provided by the environment on the basis of information collected through egocentrically organized perceptual systems.

Our proposal emphasizes the joint use of the two types of spatial information, namely, static (i.e., local views) and dynamic (i.e., about rotations and translations) information, which provide the animal with a dynamic knowledge of its environment. We assume that the various local views seen from a single location are interlinked into a panorama, via the processing of rotation information from movements of eyes, head, and whole body "on the spot." Since the firing of many hippocampal neurons is highly correlated with the rat's current location, a panorama therefore constitutes a place representation whose neural correlate is a specific hippocampal firing pattern. After exploration, the rat can, on the basis of a given local view, free itself from its current orientation and extract information about its current location with respect to the environment. Translation information is also important by introducing a sort of basic individual-scaled metrics from the minimal amount of translation resulting in a meaningful change of panorama (i.e., resulting in a change in the hippocampal firing pattern). This information processing could be further mediated by hippocampal theta cells whose firing depends on motion speed.[61,182] An additional assumption is that the firing of hippocampal place cell assemblies stores topological information in the form of synaptic strengths.[108,163] Briefly, the long-term-potentiation modifiable connections between place cells with fields that are close to

each other would be strengthened as a result of firing in close temporal contiguity. In contrast, connections between place cells that have widely separated fields stay weak because such cells cannot fire in close temporal contiguity. If this assumption is correct, then the rat's current place could come to be associated with neighboring places in various directions[31] (see section IV.C). These associations could be used by the animal to infer how the environmental perspective changes in the immediate surroundings.

On the other hand, the firing of many postsubicular cells is highly correlated with the head direction of the animal. These cells produce the same specific firing pattern whenever the animal faces the same absolute direction, no matter its specific location. There is clear evidence that the preferred direction of firing of postsubicular head direction cells is controlled by the environment.[131] Since local views depend on both the rat's location and heading, there is necessarily a process that enables the rat to free itself from its current location and extract information about its current orientation with respect to the environment. A simple solution consists of associating a common overall reference direction with each panorama.[31] This association would be established during exploration by processing rotation information (e.g., vestibular inputs) that primarily supplies the animal with the means to know which direction it faces.[16,136,179] This association would thereafter be encoded in the functional relationships between the hippocampal place cells and the postsubicular head direction cells. The idea that the postsubiculum could serve as an inertial compass directly fed by rotation information receives some support from the observation of unchanged firing patterns of head direction cells when the lights are turned off while the animal is moving in the recording arena.[131]

Once exploration is complete, static information enables the animal to extract its position with respect to the environment, while dynamic information enables it to infer the changes of location and orientation that result from its movement, and thereby to anticipate its future position. On the basis of the known properties of place and head direction cells, we propose that the hippocampal formation stores topological (rather than metric) information about the neighboring relations between the places of the current environment. In this view, the animal's current location is coded by the subset of place cells firing maximally while neighboring places are coded by the subsets of place cells that fire at a high rate, but less than maximally. As the animal moves in the environment, the subset of place cells corresponding to the animal's new current location becomes maximally active. Thus, movements within space generate dynamic information and are accompanied by moment-to-moment shifts in the active subsets of place cells. Therefore, one function of the hippocampus, besides generating place representations, would be to associate any place with its direct neighbors. Such associations would allow for anticipation of the next place knowing the current place and the direction of movement. Head direction cells would provide a directional reference that comes to be associated with place representations endorsed by place cells.

Our proposal is supported by both electrophysiological and behavioral data. The persistence of spatially selective place cell firing after the lights have been turned off or the visual cues removed[113,123,125-128] provides evidence that translation information, presumably mediated by hippocampal theta cells,[61,182] and rotation information, presumably mediated by the anterior thalamus[136,137] and the postsubiculum,[131] can be used by the hippocampus to recall the panorama associated with the rat's current place (yielded by a specific firing pattern) based on the panorama associated with its previous, neighboring, place (yielded by another specific firing pattern). As a result, the animal can keep track of its position in the dark provided it moves along a fairly short straight path (otherwise, the rat gets lost because of accumulated random errors). This ability is confirmed at the behavioral level in a place navigation task[29] (see section III.A). Other behavioral studies reveal that the ability to perform efficient place navigation based only on dynamic information requires that the rat has had extensive visual and locomotor experience of the environment.[24,25] The latter observation stresses the importance of visual information in the early stages (i.e., during exploration) of the buildup of place representations. Overall, our proposal suggests that at least part of the place navigation process can be plausibly accounted for by associative memory processes rather than by a mechanism of path representation onto a survey map of the environment.[26,31,183,184]

## VII. CONCLUSION

The influential book by O'Keefe and Nadel[61] looked for the locus of a cognitive map in the hippocampus and has resulted in a growing interest into the neural basis of animal spatial cognition. Although the present review certainly has not examined exhaustively all the neural systems likely to be involved in spatial processing, it has emphasized the complexity of the phenomena that are usually embraced under the single concept of cognitive map. Besides the nontrivial problems posed by inconsistent terminology, it is clear that the behavioral processes involved in place navigation are still a matter of controversy. The crucial empirical evidence that will determine whether rats are able to build up survey maps of their environment remains lacking. Instead, current evidence suggests that the spatial representation of the rat is strongly dependent on the possibility of the animal's collecting relevant information during exploration, serving to the buildup of spatial associations. The current limitation of behavioral models of spatial cognition in the rat is all the more disappointing since data on the neural mechanisms potentially associated with the processing of spatial information are accumulating rapidly. We currently know many pieces of the puzzle but are still far from understanding how they are put together. On the other hand, the recent finding of neurons in the primate hippocampus that have strong visuospatial correlates[185-187] supports the hypothesis that the role of the hippocampal formation in spatial processing should be extended to other mammal species. The study of the neuropsychological mechanisms of spatial cognition in the rat as a model of spatial cognition in mammals will make significant progress only if it is conceived of as a single object for research with two nondissociated aspects, corresponding respectively to behavioral and neural studies.

## ACKNOWLEDGMENTS

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