Place cells, neocortex and spatial navigation: a short review

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Abstract

Hippocampal place cells are characterized by location-specific firing, that is each cell fires in a restricted region of the environment explored by the rat. In this review, we briefly examine the sensory information used by place cells to anchor their firing fields in space and show that, among the various sensory cues that can influence place cell activity, visual and motion-related cues are the most relevant. We then explore the contribution of several cortical areas to the generation of the place cell signal with an emphasis on the role of the visual cortex and parietal cortex. Finally, we address the functional significance of place cell activity and demonstrate the existence of a clear relationship between place cell positional activity and spatial navigation performance. We conclude that place cells, together with head direction cells, provide information useful for spatially guided movements, and thus provide a unique model of how spatial information is encoded in the brain.

Keywords: Spatial memory; Navigation; Place cells; Sensory systems; Hippocampus; Parietal and retrosplenial cortex

1. Introduction

A survey of the neural substrates of spatial processing clearly highlights the important contribution of the hippocampus. Critical evidence for the hypothesis that the hippocampus carries out computations involved in navigation was initially provided by the discovery of place cells. Place cells are cells whose firing is strongly correlated with the location of a freely moving rat in its environment [42]. Anatomically, place cells are pyramidal complex-spike neurons that are found in the CA1 and CA3 areas of the hippocampus [11]. The existence of place cells converges with lesion evidence to suggest that the hippocampus might play a critical role in the processing of spatial information [43]. In this regard, place cells provide a model of how such information is encoded at a neural level.

An important issue that immediately arises is the origin of the place cell signal. Although much is known about the sensory information that is required to shape the activity patterns of place cells [48], the pathways that are involved in the transmission of this information are still poorly understood. Because the entorhinal cortex is the major area relaying the sensory information to the hippocampus, one must suspect that the cortical information reaching the entorhinal cortex is important for place cell firing. Surprisingly, however, only a few studies have looked at the contribution of neocortical areas that are connected directly or indirectly to the entorhinal cortex and hippocampus to the generation of the place cell signals. The first aim of this article is to briefly review some recent studies that have been conducted along these lines. Even though lesion studies of place cell activity make up an incomplete picture at this stage, they have revealed several important aspects of the neocortical contribution to place cell spatial firing.

Another important question is whether place cells are involved in navigation at all. Although there is voluminous evidence from the lesion literature that removing the hippocampus induces strong and permanent deficits in a wide variety of spatial tasks [43], the way hippocampal place cells are involved in navigation is still a matter of debate. The second aim of this review is to summarize recent experiments performed in our laboratory that deal with this point and demonstrate the existence of a clear functional relationship between place cell activity and spatial navigation.
2. Basic properties of place cells

Place cells are characterized by stable, spatially limited "firing fields". A place cell fires rapidly when the rat’s head is inside its field and is usually silent elsewhere in the environment. In general, place cells fire independently of the direction faced by the rat: place cell discharge recorded from a rat exploring a circular arena varies only with the rat’s location [39]. This property strongly suggests that the best correlate of place cells is the animal’s location in the current environment, and not a restricted “sensory view” of that environment.

Simple manipulations of the sensory environment in which the rat is moving reveal that several sensory channels contribute in providing meaningful input to the hippocampal place cell system. In familiar environments, place cell firing relies predominantly on visual information. In the absence of visual information, other cues, such as olfactory cues, may become important [56].

Another type of information previously suggested to be useful for updating place cell activity in the absence of visual cues is motion-related information [13,15,28, 40,49,58]. According to this hypothesis, hippocampal place cells would update their activity by keeping track of the rat’s movements in space based on signals stemming from the vestibular and proprioceptive systems as well as from motor efference copy [28]. However, this strategy, known as path-integration [32] tends to accumulate errors so that if no re-calibration occurs, the cumulative error becomes so large that any further computation is inaccurate [9,13,29,31]. This is confirmed by the finding that, when the use of external cues is precluded, motion-related (or idiothetic) cues alone are not sufficient to support spatially stable place cell firing in the long term [56].

However, idiothetic information does contribute to place cell firing as shown by our observation that blind rats have normal firing fields [55]. In this study, place cell activity was recorded while rats blind from an early age were freely moving in a cylinder arena that contained three three-dimensional objects at fixed positions near the wall of the apparatus. The cylinder itself was positioned at the center of a curtained area. The objects were different in size, shape and texture, so that they could be used as spatial landmarks likely to help rats to localize themselves in space. Blind rats had place cells very similar to those recorded from sighted rats, and, as in sighted rats [5], their firing fields depended on the objects intentionally placed into the recording cylinder as spatial landmarks. That is, the object set exerted powerful control on firing field locations as shown by the observation that rotation of the objects was followed by equivalent rotation of firing fields. Thus, place cell activity in blind rats relied on the object locations and was updated on the basis of internally generated, motion-related cues resulting from the rat’s movements in space. By inference, blind rats were aware of the object locations and were able to use motion-related information cues to update their own position relative to the objects, a suggestion that was confirmed by detailed analyses of their behavior [16]. It is likely that motion-related cues are also used by sighted rats for the ongoing calculation of their position in space. One advantage of such automatic ongoing calculation is that it puts less burden on attending to the outside environment. However, its trade-off is that it requires occasional re-calibration based on external cues so as to correct for cumulative errors resulting from idiothetic computations [48].

In summary, even though visual information is important, several inputs from motion-related systems and other non-visual modalities contribute to spatially coherent place cell firing. In the absence of vision, olfactory and tactile cues provide enough information to anchor the hippocampal representation in combination with motion-related cues.

3. Effects of neocortical damage on place cell activity

3.1. Entorhinal lesions

As noted in the introduction, few studies have addressed the effects of cortical lesions on place cell activity in spite of the strong connections that exist between the hippocampus and the cortex (see Fig. 1 for a summary of the regions of interest). The first experiment was performed by Miller and Best [30] who compared the firing patterns of place cells in normal control rats and in rats with lesions of the entorhinal cortex (lesions of the fornix, also included in this study, are not further discussed here as these fibers do not carry cortical signals). The animals were trained to run a radial maze for food reward while their neuronal activity was recorded. Lesions generally reduced the number of cells with positional correlates and the firing of those cells with clear place correlates was less robust than in normal control rats. More importantly, there was a change in the type of control exerted by environmental cues over the firing fields following 90° rotations of the maze; all units from normal rats continued to fire in the same arm

![Fig. 1. Schematic representation of major neocortical connections to the hippocampus.](image-url)
relative to the distal cues from the laboratory while only a tiny percentage of cells did so after entorhinal damage. In fact, most cells (65%) recorded from rats with entorhinal damage lost their positional correlate. The remaining cells (about 30%) still had firing fields but these were observed to stay in register with the physical arm of the maze (i.e. their location rotated with the maze rotation). This initial study indicates that loss of transmission of cortical information through the entorhinal cortex results in marked changes in place cell activity. This information seems to concern a variety of cues some of which might be related to the physical properties of the maze. Although informative, this study clearly needs to be replicated using up-to-date recording methods. This would permit better documentation of the effects of entorhinal cortex damage on several aspects of place cell discharge that it was impossible to study twenty years ago.

3.2. Perirhinal lesions

More recently, Muir and Bilkey [37] have addressed the potential contribution of another cortical area, the perirhinal cortex. This area appears to play a key role in memory [23–25], and is connected to the hippocampus both directly and indirectly via the entorhinal cortex [59]. In return, the perirhinal cortex receives projections from the entorhinal cortex, but also from widespread neocortical areas including the frontal, parietal, temporal and occipital regions as well as the retrosplenial cortex [1,2]. The firing characteristics of place cells were examined in control rats and in rats with lesions of the perirhinal cortex while they were foraging in a rectangular environment. Perirhinal damage did not reduce the number of cells that could be recorded nor did it affect place cell firing characteristics. A major effect of perirhinal damage was observed, however, when the same place cells were recorded after a delay of 24 h. While the firing fields of all place cells recorded from control rats were similar in location across successive sessions, many fields from rats with perirhinal cortex lesions were found to shift position across the delay period. Therefore, even though the perirhinal cortex is not necessary for the initial formation of firing fields in the hippocampus, it seems required for the maintenance of stable fields over time. This result suggests a role of the perirhinal cortex in the reliable identification of the current environment, based on the memory of cues and associations of cues from that environment.

3.3. Visual cortex lesions

Because hippocampal place cells rely on both visual and motion-related information to maintain stable firing fields (see above), we recently have started to look at the consequences of neocortical damage in areas concerned with the processing of such information. As shown in the previous section, place cell activity is not strongly altered when the rat is deprived of vision early in its life [55]. Even though the preserved properties of place cell firing can be explained by compensation mechanisms such as learned sensory substitution, this finding suggests that vision might not be so essential for navigation, a conclusion supported by the observation that spatial performance in blind rats is not profoundly impaired in water maze navigation [22]. In view of the relatively preserved spatial skills in blind rats, it seems therefore somewhat unexpected that ablation of the visual cortex induces a strong deficit in radial maze performance [10,26]. A direct comparison of rats with visual cortical damage and blind rats revealed a much stronger impairment in the brain-damaged rats [12]. This impairment suggests that the visual cortex might accomplish some central function in spatial processing. To examine this possibility, we recorded place cells from rats with lesions of the visual cortex [47]. The procedure was similar to that used by Save et al. [55] with blind rats (see Section 2), therefore making it possible to compare place cell discharge in rats with visual cortex lesions and normal sighted or early blind rats. Thus, place cell activity was recorded while rats were freely moving in a cylinder with three objects near the wall of the apparatus.

Rats with visual cortex lesions were found to have functional place cells whose fields were similar to the fields recorded from rats with an intact cortex and were stable across time. Contrary to both normal sighted rats and early blind rats [5,55], however, place cells from rats with visual cortex lesions were shown to use three-dimensional objects much less efficiently for the spatial anchoring of firing fields. In rats with an intact visual cortex, rotation of the objects is followed by equivalent rotation of firing fields in a vast majority of instances. That is, the object set exerts almost ideal control on firing field locations. We found that this control is dramatically reduced in rats with visual cortex lesions: in these animals, rotations of the object set only rarely induced coherent field rotations. Thus, control rats used the objects within the recording cylinder as the reference frame for anchoring their firing fields whereas rats with visual cortex lesions used some uncontrolled, but stable cues stemming from the experimental room. Because their inability to use the objects was partial, however, this effect can be best described as an alteration rather than a total disruption of the process that selects the spatial reference frame. A simple explanation of this effect is that rats with visual cortex damage may rely on non-visual distant information (such as odors or sounds) to set the reference direction for firing fields. However, a more interesting possibility is that the visual cortex might be involved in the initial calibration of the spatial reference frame used by the place cell system. For
example, it might be required for selecting the visual cues to use as landmarks. Interestingly, disrupted cue control over place cell firing fields is also observed after lesions of the postsubiculum [60], thus raising the possibility that both the visual cortex and postsubiculum work together to provide the angular reference direction for orienting the hippocampal spatial map. Such a function would explain the altered cue control properties of place cells as well as the spatial deficits seen after visual cortex lesions [12,55].

3.4. Retrospl enial and parietal cortex lesions

Both the parietal and retrospl enial cortices are hypothesized to contribute to the integration of visuo-spatial and motion-related cues for navigation [33,57]. These two structures receive visual afferents from secondary visual sensory cortical regions and are connected to a number of structures in the hippocampal formation such as the entorhinal cortex, the subiculum and the perirhinal cortex [1,64]. In addition, lesion of either cortical region has been shown to induce deficits in spatial tasks [14,57]. Accordingly, the parietal and retrospl enial cortical areas might exert an influence over hippocampal place cell activity. This has been confirmed in a recent study by Cooper and Mizumori [6] who examined the effects of temporarily inactivating the retrospl enial cortex on place cell activity in rats performing a radial maze task. The consequences of such inactivations were examined during acquisition and during retention of the task. In addition, for the retention group, the animals performed the task in light or in darkness. The authors found that retrospl enial inactivations disrupted the stability of firing fields, i.e. the preferred location of firing fields shifted to unpredictable locations of the maze, in both acquisition and retention. Interestingly, these firing pattern modifications were correlated with performance deficits during acquisition and during retention in darkness only. This suggests that cooperation between the retrospl enial cortex and the place cell system is required for different stages of spatial information processing, including initial integration of visuo-spatial and movement-related sensory cues and the use of mnemonic visuo-spatial information in the absence of environmental cues [33]. Interestingly, the retrospl enial cortex is part of a large network of connected brain structures that includes the postsubiculum and the anterior thalamic and lateral dorsal thalamic nuclei. All these areas contain head direction cells that fire when the rat’s head faces a specific direction independently of its location [3,60]. Since head direction cells and place cells are strongly coupled [18], it is possible that the effects of retrospl enial inactivations on hippocampal place cells were mediated by the disruption of the head direction system. In support of this hypothesis, lesions of the postsubiculum are observed to disrupt cue control of hippocampal firing fields (unpublished observations reported in [60]).

The parietal cortex (formerly area 7 in Krieg’s terminology [19]) has reciprocal connections with the retrospl enial cortex and is indirectly connected to the hippocampus [62]. In our laboratory, we have recently examined the effects of parietal cortex lesions on place cell activity (unpublished data). Parietal-lesioned and control rats were allowed to forage freely for randomly scattered pellets in a recording cylinder. Three objects, similar to those used in a previous study [47], were placed against the wall of the cylinder to serve as landmarks in a cue-controlled environment. Contrary to retrospl enial inactivations, parietal cortex lesions did not impair firing field stability in standard conditions. In addition, rotation of the object set was accompanied by an equivalent rotation of firing fields, showing that parietal rats used the objects to maintain firing field stability. The most dramatic effect of parietal cortex damage was observed during the session that followed the rotation test, when the objects were removed in presence of the animal. In the absence of object landmarks, a substantial number (48%) of firing fields in parietal-lesioned rats (15% in control rats) shifted back to the initial, standard, pre-rotation location (Fig. 2). In control rats, most firing fields remained stable relative to the rotation session (36%) or disappeared, i.e. cells stopped firing (27%). Thus, these results suggest that field stability in control rats was strongly dependent on the objects whereas field stability in parietal-lesioned rats could be placed under the control of background cues when the objects were removed. This raises the possibility that the parietal cortex is involved in the processing of proximal landmarks and contributes to provide some stable local frame of reference to the hippocampal place cell system. Another complementary explanation is that parietal-lesioned rats rely on background cues because they are unable to use motion-related cues to maintain firing field stability in absence of objects. Interestingly, these results together with those obtained in rats with damage to the visual cortex suggest that the processing of visuo-spatial information along the occipito-parietal axis results in the calibration and selection of the reference frames used by the place cell system to anchor stable firing fields.

3.5. Commentary

This short review of lesion-induced alterations of the place cell signal reveals a striking parallel with the behavioral spatial deficits that result from damage to the corresponding cortical areas. Virtually any cortical area shown to be important for performance of spatial navigation tasks can be demonstrated to be also important
for the generation of normal place cell characteristics. Because spatial behavior is so easily disrupted by brain damage, it is often difficult, however, to determine the exact nature of the processing stage that has been affected by the lesion. With regard to this point, considering the place cell system as a model system that, among other tasks, is a spatial information processing module and looking at the changes in place cell discharge provides a way of characterizing cortical contributions in a much better defined manner. Although at this stage it may be speculative to propose specific functions for each cortex, it appears that the effects of damage to each cortical area on place cell discharge match the deficits expected from known neuroanatomical and behavioral data.

4. Relationships between place cell activity and spatial behavior

Place cells continuously indicate the rat’s location in the current environment. This property is the cornerstone of the cognitive map theory of hippocampal function [43]. This theory is further supported by the observation that destruction of the hippocampus disrupts the performance of rodents in a wide variety of spatial tasks [16,36,54]. Thus, both unit recording studies and lesion work converge to indicate a central role for the hippocampus in map-based navigation. Other evidence suggesting that place cells are the essential units of the putative environmental map come from the observation that manipulations that produce alterations of place cell properties also impair performance in place navigation tasks. For example, genetically modified mice with an impaired long-term potentiation (LTP) as well as rats with a treatment-induced impaired LTP have abnormal place cells and reduced performance in place navigation tasks [4,17,27,34,51,52]. Thus, treatments that generate place cell abnormalities seem to reliably induce abnormalities of spatial navigation.

Although these findings support the mapping theory, the weaknesses associated with lesion-type methods imply that a more direct approach is required to show how the place cell signal relates to behavior in a normal animal. Probing the relationship between place cell discharge and the rat’s spatial behavior requires concomitant recording of both events. Surprisingly, the existence of a direct relationship between place cells and navigation was only anecdotally noticed [44]. Rats were trained to reach one arm of a plus-shaped maze on the basis of its location relative to a set of extra-maze cues. On a few occasions, these cues were removed. Under these circumstances, it was found that even on error trials the rat’s random choice of goal remained in register with its place cell firing fields, suggesting that place cell activity and spatial behavior were coupled. To explore this issue in a more systematic way, we performed two studies both of which relied on the same underlying principle: if place cells provide position information useful for performing a spatial task, then behavioral manipulations that result in the place cell information being out of register with that task should also lead to incorrect spatial behavior.
4.1. Place cell activity in a spatial memory task

The contribution of place cell activity was first probed in a spatial alternation task, known to depend on the integrity of the hippocampus. Rats were trained to perform a continuous spatial alternation task in a Y-shaped maze in which the only available landmark was a prominent white card, positioned between two arms [21]. In this task, the rats had to alternate between the two arms of a Y-maze to get a food reward in the third (goal) arm (Fig. 3A). Once the rats performed well in the presence of the card (“standard condition”), place cells were recorded in several sessions after the card was rotated or removed. These manipulations were expected to result, on some occasions, in the angular positions of firing fields shifting out of register with the positions seen in the standard condition. Our purpose was to determine if the rats’ performance was worse when fields were out of register relative to their standard position.

Overall, the results confirmed the existence of a strong deterioration in performance when field positions were inconsistent with the learned task. First, the number of correct responses was dramatically reduced with rats being rewarded, on average, half as often during sessions with consistent field placements. Second, the nature of the errors was also different when fields were out of register with the task, with rats either repeating incorrect choices of an individual arm or failing to follow the basic alternation rule to solve the task. These types of errors reflect a more complete disorganization than just making the most commonly observed alternation (working memory) errors. Third, erroneous placements of firing fields often predicted erroneous visits to an individual arm.

Together, these results show that erroneous field placements were associated with disorganized spatial behavior. Noticeably, the changes in firing fields concerned only their angular position in the maze: even though the fields were on the wrong arm relative to the goal, their radial position relative to the maze center was correct. In addition, all fields were coherent with one another when several cells were simultaneously recorded. Thus, there was no evidence that cue manipulations resulted in the activation of a different representation, as is the case when place cells are recorded in several differently shaped environments [38]. Instead, the same place cell representation was active, but was incorrectly oriented with respect to the spatial task the rat had to accomplish. Thus, a reasonable assumption is that the observed behavioral effects were caused by the mismatch between the orientation of the hippocampal representation and the learned task, rather than by the activation of a distinct representation.

Interestingly, very similar findings were observed for head direction cells whose activity was recently demonstrated to correlate with spatial behavior on a radial maze [7]. Head direction cells fire only when the rat is heading at specific directions independently of its current location and are found in several brain areas (such as the postsubiculum and anterior thalamic nuclei) all of which have extensive connections with the hippocampus [60]. Animals implanted for head direction cell recordings were trained to find reward on a particular arm in a fixed position relative to a visible cue in the room.

Fig. 3. Behavioral procedures used to probe place cell involvement in spatial performance and general principle. (A) The continuous spatial alternation task [22]. The apparatus is a Y-shaped maze with a large cue card (shown as an arc) as the single spatial landmark. The circle at the end of arm C indicates the location where the rat was rewarded with a food pellet if it had previously made a correct alternation visit to one of the other two arms A and B. (B) The place preference task [21]. The apparatus is a cylinder with a single cue card attached to the wall (shown as an arc). The rat had to enter an unmarked goal zone and stay there to trigger the release of a food reward from a dispenser situated above the cylinder. Since the released pellet could land anywhere in the cylinder, the rat had to leave the goal area to find the pellet. The small circle shows the goal location in the Far task. In the Near task, the goal area was beneath the cue card while in the Cue task, it was directly signaled by a black disk on the floor. The rat’s path to the goal is shown as a continuous line. The path away from the goal to retrieve the food pellet at location ‘x’ is shown as a dashed line. (C) The general principle of the experiments combining place cell recordings and the analysis of navigation performance is illustrated for the Far task. A schematic place cell firing field (shown as a set of concentric gray-shaded ellipses) represents the orientation of the hippocampal map. The purpose is to determine where the rat will search for the goal when a cue manipulation (here a rotation of the cue card) does not produce the expected rotation of the firing fields (i.e., of the hippocampal map). One prototypical situation in which the hippocampal map often fails to re-orient relative to the external environment is when the card is rotated in the presence of the rat. Under these circumstances, the goal location indicated by the external environment (C’ for cue-referred) is distinct from the goal location indicated by the hippocampal map (F’ for field-referred). The results show that rats look for the goal at the field-referred location (i.e., their choices are based on the hippocampal map) only when they have to rely on a spatial representation of the goal location (i.e., in the Far task), but not in other conditions (see text and [21] for details).
the cue was rotated to another fixed position in the room, both the animal’s choice of maze arm and the head direction cell’s preferred direction shifted in concert relative to the cue. However, on some infrequent trials, the head direction cell’s preferred direction remained stable relative to background cues in spite of the cue rotation. In these instances, it was observed that the rat’s choice also stayed stable relative to the rotated cue, thus remaining in register with the head direction signal. Overall, these findings indicate that both place cells and head direction cells play a role in guiding navigation.

4.2. Place cell activity in spatial and non-spatial navigation tasks

The cognitive map theory predicts that hippocampal integrity is more critical for place navigation than for orientation based on simpler mechanisms such as orienting to beacons. This hypothesis is supported by the finding that hippocampal lesions disrupt place navigation but not beacon navigation [35,41,45]. To address a similar issue at the place cell level, we looked at performance by normal animals in place and beacon navigation tasks after environmental manipulations that disturb the relationship between the place cell representation and the cues used to solve the problems. The theory predicts that such disturbances will disrupt performance of place navigation but not of beacon navigation. To test this prediction, rats were trained in several tasks that required either map-based place navigation or simply heading towards a strong marker stimulus [20].

We used the place preference paradigm developed by Rossier et al. [50]. In this task, rats have to enter an unmarked goal designated by the experimenter as the goal, which then triggers release of a food reward from a dispenser situated above the circular arena (Fig. 3B). The rat then has to move away from the goal area to retrieve the food pellet wherever it ended up in the arena. The only spatial landmark is a salient white card attached to the wall of the arena. Three distinct conditions were used with different rats. In the Far condition, the goal was away from the wall card so that the rat had to use a place strategy, i.e. to infer the goal location from its spatial relationship with the card. In the Near condition, the goal was located beneath the wall card so that all the rat had to do was to move towards the card (though it could use a place strategy as well). Finally, in the Cue condition the goal was directly signaled by a mark (a black disk) on the floor. The mark was moved from one session to another (thus making the wall card irrelevant for solving the task) so that the solution required a guidance strategy.

Place cells were recorded while rats performed the task. To modify relationships between visible stimuli and place cell activity, we made “hidden” or “visible” 90° rotations of the card on the cylinder wall and, when present, independent rotations of the disk on the cylinder floor. Hidden rotations were made with the rat removed from the cylinder and caused 90° firing field rotations in a vast majority of sessions (>80%). Visible rotations were made while the rat was inside the cylinder and, as expected [53], caused field rotations only in minority of sessions (<30%). In the latter condition, the failure of fields to rotate is caused by the conflict between motion-related and cue-related information that is generated by the visible card rotations. More importantly, visible card rotations generally induced firing fields to shift out of register with the new goal location (as defined by the rotated card location) while hidden card rotations generally induced firing fields to stay in register with the new goal location.

In all conditions, each session started with a period during which the feeder was switched off, irrespective of the animal’s response. This partial extinction procedure was used to let the animals search without any feedback information about the goal location and thus allowed us to determine where the rat “thought” the goal was located (Fig. 3C). The results of the different conditions were contrasted. A strong decrease in performance was observed in the Far condition when fields were out of register with the card-referred goal. Most rats tended to search for the goal in the field-referred rather than card-referred goal location. In contrast, a modest decrease in performance was observed in the Near condition when fields were out of register with the card, with rats searching for the goal at the card. Finally, field placements had no effect whatsoever on performance in the Cue condition in which the goal was directly signaled by a movable mark on the floor.

In summary, we found that visible rotations tended to disrupt the relationship between firing fields and cues in all tasks but impaired performance only in the spatial problem that required map-based navigation. Thus, it appears that the correct orientation of the hippocampal map with the external stimuli is essential for efficient performance in a navigational task but not in guidance or beacon navigation tasks. Noticeably, reliable place cell firing was observed in all tasks, i.e., whether or not the rat had a spatial navigation task to accomplish (see also [61]). Therefore, place cells continuously provide background information as to the rat’s location, yet this information appears critical only for true spatial navigation. We therefore conclude, as proposed by the spatial theory of hippocampal function that the rodent hippocampus participates in solutions of place navigation tasks but not of simpler guidance tasks.

5. Conclusion

This review addressed issues about the cortical origin of the place cell firing patterns and about the functional
significance of place cell activity. As to the first of these two issues, several cortical areas appear to subserve complementary functions in the generation of place cell firing. For example, the perirhinal cortex is required for long-term stability of firing fields [37]. The retrosplenial cortex appears to be important for the initial processing of spatial cues but would also be needed for the mnemonic use of these cues to guide navigation when they have been removed [33]. In contrast, the visual, parietal and entorhinal cortices appear to be involved in the selection of cues necessary for the spatial anchoring of firing fields; the three areas seem to process separate aspects of space, with the entorhinal cortex being more involved in processing distal cues [30,46], the visual and parietal cortices dealing with the local aspects of the environment explored by the rat [47]. Although this description is schematic, it has the advantage of providing a framework within which more refined functions can be worked out. It seems to us, however, that such refinement will require more standardized procedures for recording place cell activity among different laboratories.

With regard to the issue of the functional significance of place cell activity, we provided strong evidence that place cell signals are crucial when the animal needs to “know” its own position and the positions of other objects. An important issue, however, is whether place cells directly guide navigation, or are just one component in a larger network of structures more actively involved. In the latter and more likely view, the network would probably have to include not only brain areas in which head direction cells were found [60], but also areas known to be involved in behavioral decisions in an essential way (e.g., prefrontal and parietal cortex).

Another difficulty with the correlational approach that underlies our research is that it does not reveal what hippocampal cell firing patterns would signal in non-spatial complex tasks. Thus, it is difficult to determine the generality of this conclusion. In particular, it is known that hippocampal cells have behavioral correlates in non-spatial tasks, therefore suggesting that the hippocampus is involved in the processing of both spatial and non-spatial relational information [8,63]. Yet the specificity of the hippocampal cell signal, as well as the properties of head direction cells and the strong coupling that seems to exist between the two populations of cells [18], make it very likely that an important function of this system is to process spatial information for navigation.

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