HIPPOCAMPUS 10:491–499 (2000)

Hippocampal-Parietal Cortical Interactions in Spatial Cognition

Etienne Save* and Bruno Poucet

Center for Research in Cognitive Neuroscience, Centre National de la Recherche Scientifique, Marseille, France

ABSTRACT: Growing evidence suggests that the associative parietal cortex (APC) of the rat is involved in the processing of spatial information. This observation raises the issue of the respective functions of the APC and the hippocampus in spatial processing as well as of their possible interactions. In this paper, we review neuroanatomical, electrophysiological, and behavioral data that support the existence of such functional interactions. Our hypothesis is that the APC is involved in the initial combination of visuospatial information and self-motion information necessary for the integration of egocentrically acquired information into allocentrically coded information, the latter step being completed in the hippocampus. The dialogue between the hippocampus and the APC is therefore crucial, particularly when the elaboration and/or updating of an allocentric representation depends on complex combinations of visuospatial and self-motion information. *Hippocampus 2000;10:491–499.* © 2000 Wiley-Liss, Inc.

KEY WORDS: hippocampus; parietal cortex; spatial cognition; rats

INTRODUCTION

For many years, studies of the neural bases of spatial cognition in animals have focused on the role of the hippocampus. The dramatic effects of hippocampal lesions in spatial tasks as well as the existence of place cells provide strong evidence that the hippocampus is crucially involved in spatial processing (O'Keefe and Nadel, 1978). Although it is acknowledged that the hippocampus may not be involved in all types of spatial processing, the possible contribution of other brain areas has been mostly neglected. In particular, the idea that the associative parietal cortex (APC) might be specifically implicated in spatial perception and cognition is relatively recent.

Early studies on the role of the APC in rodents were mainly motivated by the issue of whether there is some functional homology between the posterior parietal lobes in primates and the parietal cortex in rodents (Thomas and Weir, 1975; Boyd and Thomas, 1977). In humans, damage to the posterior parietal lobes induces a complex syndrome made of a constellation of cognitive deficits in numerous spatial abilities (reviewed in Lynch, 1980). Basically, investigators were concerned with the possibility that the rat may provide a useful model of some basic aspects of the primate parietal syndrome. The objective of rat studies was thus to assess the effects of parietal lesions in spatial (maze learning) and nonspatial (pattern discrimination) tasks. Significant data have accumulated over more than 10 years, but many aspects of the neuroanatomical and functional organization of this cortical area are still unknown. Several hypotheses regarding the role of the APC in spatial cognition have been proposed but, so far, none of them accounts satisfactorily for the diversity of experimental findings.

If the APC plays a specific role in spatial processing, then it can be asked what are the respective contributions of the hippocampus and APC to spatial cognition, and beyond that, what are their functional relationships? Indeed, it is hard to imagine that these two structures might play a role in the same processing domain without interacting, even if they contribute to different processing systems. In the present paper, we briefly examine how the neuroanatomical and functional data support the existence of a functional interaction between the hippocampus and the APC. Because to some extent the nature of the functional interactions can be inferred from observed anatomical relationships, we first summarize the most important connecting pathways involving the APC and the hippocampus (see Corwin and Reep, 1998, for a more extended review on the pattern of connections of the APC). We then present some behavioral data on the respective contributions of these two structures to spatial processing, and we suggest that they do cooperate. On the basis of these data, we propose a hypothesis in which the APC performs associative processing between visuospatial and movement-related information. Such an associative process would initiate the incorporation of egocentric-coded sensory inputs into allocentric-coded representations which are implemented in the hippocampus. The parietal-hippocampus functional axis seems to be particularly important when the elaboration of a representation depends on complex combination between visuospatial information and self-motion information.

NEUROANATOMICAL INTERACTIONS BETWEEN THE APC AND THE HIPPOCAMPUS

Until recently, lesion studies on APC function were weakened because the existence of a specific parietal area was still questioned.

---

*Correspondence to: E. Save, Center for Research in Cognitive Neuroscience, CNRS, 31 chemin Joseph-Aiguier, 13402 Marseille cedex 20, France. E-mail: save@lnf.cnrs-mrs.fr

Accepted for publication 1 May 2000

Neuroanatomical arguments supporting the existence of the APC in the rat were first provided by Krieg (1946), who analyzed the cytoarchitecture of the rat neocortex. Krieg (1946) also suggested that the APC (which he called "area 7") could have an associative function between "somesthetic and visual sensations." This anatomical organization was confirmed much later by Kolb and Walkey (1987) and Reep et al. (1994), who studied the thalamo-cortical and cortico-cortical connections of the presumed parietal cortex. Studies using retrograde degeneration or, more recently, axonal tracing techniques provide a very consistent pattern of thalamic inputs. Thalamic afferents involve the lateral dorsal, lateral posterior, and posterior nuclei (McDaniel et al., 1978; Chandler et al., 1992). In contrast with the visual areas or somatosensory areas, the APC does not receive projection from the ventrobasal and dorsal lateral geniculate nuclei (Chandler et al., 1992; Reep et al., 1994). Most importantly, injections of retrograde tracers in the parietal area and connected structures allowed researchers to determine the cortico-cortical connections of the APC and to distinguish this area from the secondary visual areas (Kolb and Walkey, 1987; Reep et al., 1994). As shown in Figure 1, the APC has connections with frontal areas (Fr2), ventrolateral and medial orbital areas (VLO and MO, respectively), somatosensory areas (Par1 and Par2), secondary visual areas (Oc2M and Oc2L), temporal auditory areas (Te1), and the retrosplenial cortex (nomenclature according to Zilles, 1985). Notably, the connections with the frontal, orbitofrontal, and visual areas are bilateral (Corwin and Reep, 1998). From a functional point of view, the patterns of thalamo-cortical and cortico-cortical connections strongly suggest that the APC is a multimodal structure which performs associations between visual and somatosensory information.

The issue of whether the APC receives vestibular inputs is intensely debated. Although to our knowledge there is no report showing such connections in the rat, we know from cat and monkey work that vestibular information projects, via specific thalamic nuclei, to the somatosensory and parietal cortices (reviewed in Fukushima, 1997). In particular, vestibular responses have been recorded in the posterior parietal cortex (area 7) in monkeys (Kawano et al., 1980). In addition, Guldin et al. (1992, 1993) showed in rats (and in monkeys) that there are monosynaptic projections from several cortical areas, including the parietal cortex, to the vestibular brainstem nuclei. The existence of direct projections from the vestibular nuclei to the rat neocortex is still questioned. Although the neuroanatomical organization of the rat vestibular system needs qualification, these findings are compatible with the hypothesis that the APC processes vestibular information in addition to visual and somatosensory information. Functionally, this is consistent with a number of behavioral and electrophysiological results showing that parietal function is related to the processing of idiothetic information (Save and Moghaddam, 1996; Chen et al., 1994a,b; see below). An attractive hypothesis is that the APC would provide vestibular information to the hippocampal formation (Smith, 1997).

Neuroanatomical relationships between the APC and the hippocampus are indirect. They involve a number of intermediate structures which participate in the processing of spatial information. The APC is connected with the retrosplenial cortex (Reep et al., 1994),which is itself interconnected with the subicular complex of the hippocampal formation and projects to the entorhinal cortex (Witter, 1993). In addition, the retrosplenial area receives projections from rostral thalamic nuclei such as the anteromedial, laterodorsal, and lateroposterior nuclei. Visual information may also be provided to this area via projections from the primary and secondary visual areas (Wyss and Groen, 1992). The contribution of the retrosplenial cortex to spatial processing in rodents has been shown in a number of lesion studies (Sutherland et al., 1988; Meunier et al., 1991; Cooper and Mizumori, 1999). Most interestingly, this structure contains cells whose firing is correlated with the rat head direction in space (Chen et al., 1994a) and is probably part of a functional network including at least the APC, the hippocampal formation (postsubiculum), and the thalamus (lateral dorsal and anterior dorsal nuclei), where head direction cells have been also recorded (Taube et al., 1996). In addition, the directional signal provided by the head direction cells in these brain regions is strongly influenced by vestibular inputs, as is the positional signal provided by hippocampal place cells whose firing is location-specific (Sharp et al., 1995). This suggests that one major component of the hippocampal-cortical interaction is related to the processing of vestibular information.

In summary, the organization of the neural circuitry between the APC and the hippocampus sheds some light on the nature of their functional interactions. The pattern of cortico-cortical connections suggests that the APC combines visual, somatosensory, and probably vestibular information. Idiothetic information (vestibular, somatosensory, but also proprioceptive information and motor efference copy) is provided by the rat self-motion. Interestingly, the retrosplenial cortex seems to perform the same type of encoding as does the APC, i.e., the integration of visual and idiothetic cues. Further research may reveal some behavioral dissociation of lesion effects, suggesting that each structure participates in a specific aspect of an overall process. According to this view, the combination of visual and idiothetic information proceeds along the parietal-retrosplenial axis and eventually reaches the hippocampus. We hereafter examine how the behavioral and electrophysiological results can be reinterpreted in the light of this hypothesis.

BEHAVIORAL AND ELECTROPHYSIOLOGICAL APPROACH TO APC-HIPPOCAMPUS INTERACTIONS

Few studies have investigated the functional interactions between the APC and the hippocampus, e.g., by making simultaneous electrophysiological recordings in both structures as the animal performs a behavioral task (Qin et al., 1997). Most often, hypotheses on parietal-hippocampal interplay have to be deduced from the direct (within the same study) or indirect (from separate studies) comparisons of the effects of APC and hippocampal lesions in spatial tasks.

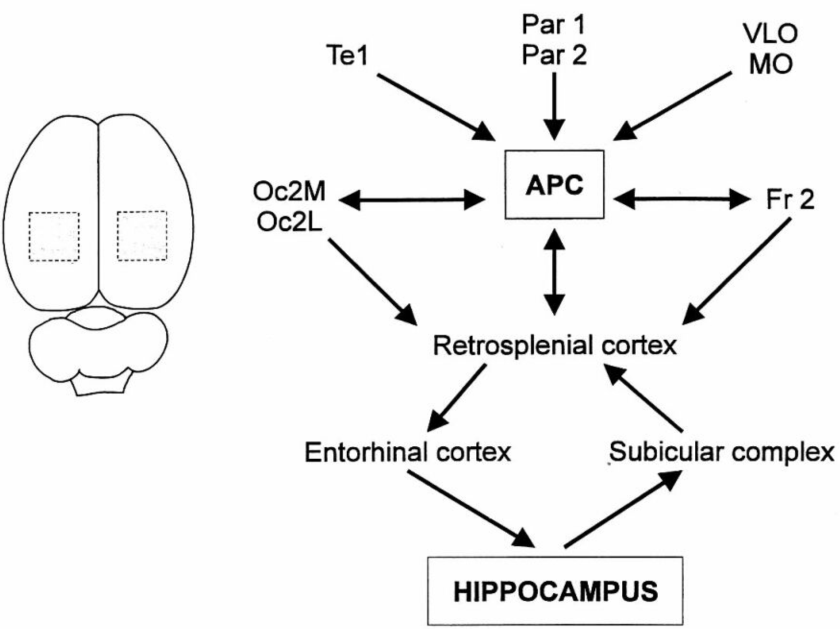

FIGURE 1. Left: View from above of a rat brain, showing the extent of the APC according to Kolb and Walkey (1987). The stereotaxic coordinates relative to Bregma are AP −2 to −6 mm and L +1.5 to +5.5 mm. Right: Main cortico-cortical connections between the APC and the hippocampus. The connections between the APC and other cortical areas are also shown.

Processing of Visual Information

The existence of cortico-cortical connections with the primary and secondary visual areas strongly suggests that visual information is a major component of APC function. Surprisingly, only a few studies have focused on the nature of the visual information that would be processed by this structure. These studies provided very contradictory results as to the effects of APC lesions in visual or visuospatial processing abilities in rats (Boyd and Thomas, 1977; McDaniel et al. 1979; Davis and McDaniel, 1993; McDaniel and Skeel, 1993). However, it seems that rats with APC lesions do not have gross visual disabilities. For instance, they are able to discriminate among and recognize objects (Kolb, 1990; Kolb et al., 1994; Save et al., 1992). Therefore, we speculate that the APC may manage complex visual information, preprocessed by the visual cortices, and including some of the spatial features of particular views of the environment. Interestingly, a number of studies suggest that the APC is not involved in the perception of relatively elementary spatial features such as allocentric or egocentric distances (Long and Kesner, 1996, 1998). In contrast, APC lesions affect the perception of multiple object scenes (DeCoteau and Kesner, 1998), particularly when familiar objects are displaced to a new location or when new objects occupy a new location. This suggests that the APC deals with complex visual features of the environment, in particular those combining the stimuli and the places. This view is consistent with the fact that in monkeys, single-unit activity in posterior parietal area 7 is mainly influenced by the location of stimuli in space rather than by their specific features (Andersen et al., 1985). Accordingly, visuospatial processing could involve the parietal pathway both in the rat and in primates (Ungerleider and Mishkin, 1982).

Although the hippocampus does not receive direct projections from the visual cortices, there is a large body of data showing that the hippocampus incorporates visual information. In particular, place-cell activity has been shown to be controlled by visual cues (reviewed in Muller, 1996). However, unlike head direction cells, place cells fire irrespective of the direction of the animal's head, i.e., they do not respond to a specific view of the environment. Instead, they respond to the views available from a given viewpoint with a 360° rotation angle. Linking the successive local views via self-motion signals allows the animal to elaborate a place representation (Poucet, 1993).

Processing of Idiothetic Information

The idea of a self-motion component in the APC function is less well supported by neuroanatomical data than that of a visual component. In a behavioral study, Save and Moghaddam (1996) trained rats with APC lesions in the water maze navigation task from a constant starting point and in total darkness. Performance in this task, therefore, depended exclusively on the use of self-motion cues. Postsurgery-trained APC rats were impaired in acquisition but, interestingly, presurgery-trained APC rats were not significantly impaired in retention. Hippocampal rats have not been tested in this situation. The ability of APC rats to use a motoric response was also investigated by McDaniel at al. (1995). Rats with APC lesions in either the left or right hemisphere were trained in a response learning task in the water maze. Both lesion groups were deficient relative to control rats. Together, these results suggest that the APC contributes to the processing of self-motion cues.

Self-motion cues, and in particular vestibular cues, have been shown to be necessary for the "path integration" navigating system. This system performs integrations of linear and angular acceleration and allows the animal to track its position relative to a starting point in the absence of any external cues (Etienne et al., 1996). Although the deficit shown by Save and Moghaddam (1996) could reflect a dysfunction of the path integration system, further experiments aimed at specifically testing this ability are needed. Support for an involvement of the APC in the processing of self-motion information has arisen from electrophysiological data. Head direction cell activity, as reflected by the cells' spatial tuning, has been found to be modulated by idiothetic cues in the APC, retrosplenial cortex (Chen et al., 1994a,b), and anterior thalamus (Blair and Sharp, 1996). The properties of head direction cells strongly suggest that they participate in the path integration processes (McNaughton et al., 1991; Blair et al., 1997; Golob and Taube, 1999).

The issue of the possible function of the APC in path integration is crucial in particular with respect to the function of the hippocampus. Indeed, several recent lesion studies support the hypothesis that the hippocampus is necessary for path integration (Whishaw and Tomie, 1997; Whishaw and Maaswinkel, 1998). However, another study (which differs from the above two studies in terms of locus, extent of lesions, and nature of the tasks) reported that rats with hippocampal lesions are mostly unaffected in their ability to path integrate (Alyan and McNaughton, 1999). Support for the path integration hypothesis of hippocampal function also comes from place-cell recording studies, which show that idiothetic cues can exert a control over place-cell activity (Knierim et al., 1998; Sharp et al., 1995; Wiener et al., 1995). Markus et al. (1994) found that place fields of CA1 cells remained stable in darkness, although they were less reliable than under light.

In summary, both the APC and the hippocampus seem to share similar functional properties. Both structures process idiothetic information, and both are also influenced by visual information provided by external landmarks. Altogether, these findings suggest firstly that idiothetic cues constitute one of the main sources of spatial information for the animal, and secondly that the APC and the hippocampus are part of a functional network devoted to the managing of self-motion and external cues (see also Blair and Sharp, 1996). The hypothesis of the involvement of these structures in a common processing system is further supported by Golob and Taube (1999). They found that both hippocampal and APC lesions prevent the head direction cells from maintaining a similar preferred direction when moved from a familiar to a novel environment.

Combination of Visual and Idiothetic Information

The existence of several brain regions that cooperate in processing visual and self-motion information suggests that the combination of these two sensory sources of spatial information is at the core of spatial processing. In particular, such a combination is crucially involved when the animal explores a new environment. In this situation, a rat displays a variety of behavioral responses, suggesting that it collects visual (but also olfactory, auditory, and tactile) information at particular viewpoints. The perception of these panoramic views (also termed local views; see McNaughton et al., 1991; Poucet, 1993) depends on the relative position of the animal and therefore relies on an egocentric coding of space. Successive local views are linked by the specific movements (and associated optic flow) required to go from one viewpoint to another. The redundancy of such process involving multiple viewpoints and trajectories eventually leads the animal to extract the spatial invariants of the environment and therefore to elaborate an allocentrically coded representation of space. Accordingly, one expects that both parietal and hippocampal lesions would elicit a deficit in such a process. Using an exploratory dishabituation paradigm, we investigated the ability of lesioned and control rats to memorize and recognize, through exploration, the spatial arrangement of a set of objects (Save et al., 1992). Rats had to explore during successive sessions a circular arena containing five distinct objects. Five sessions were used for habituation and for the sixth session, the spatial arrangement was modified and the exploratory reaction to the spatial change was assessed (Fig. 2A).

Both hippocampal and parietal rats displayed a control-like habituation but were unable to detect the spatial change (Fig. 2B). The hypothesis of a general memory deficit could be ruled out, since all rats were able to identify a novel object replacing a familiar one. Instead, the results suggest that the hippocampal and parietal rats were impaired in the elaboration and/or use of a spatial representation of the environment. One possible interpretation is that their ability to combine visual and idiothetic information during the habituation phase was affected by the lesions. However, these results may also be accounted for by a role of the APC and hippocampus in other stages of spatial information processing (e.g., comparison between a stored representation and the actual environment, or updating of a representation). In any case, the absence of dissociable behavioral effects of hippocampal and APC lesions suggests that these two structures have intricate functions.

The dishabituation procedure has been used likewise to study the effects of hippocampal and APC lesions in the C57BL/6 (C57) and DBA/2 (DBA) inbred strains of mice. These two strains constitute a very interesting experimental tool. Indeed, behavioral and

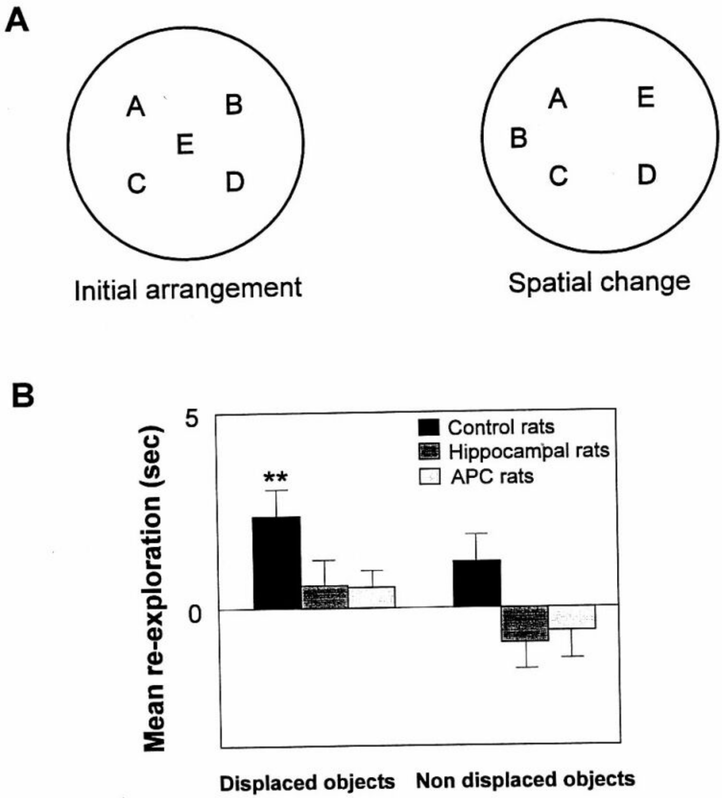

FIGURE 2. A: View from above of the circular arena, containing five distinct objects (A, B, C, D, and E). Three groups of rats (control, hippocampal, and APC rats) had to explore the initial arrangement of objects during successive sessions. Following habituation, the spatial configuration of the set of objects was modified (spatial change): two objects out of five were displaced (B and E). The exploratory reaction to the spatial change was examined. B: Mean re-exploration (in seconds) of the displaced and nondisplaced objects following the spatial change. Positive bars indicate that the rats explored the objects more during the "spatial change" session than during the last "habituation" sessions. Control rats displayed a significant renewal of object exploration (asterisks) selectively directed at the displaced objects, whereas the hippocampal and APC rats did not re-explore either kind of objects. They were not able to detect the spatial change (from Save et al., 1992).

neurobiological data support the hypothesis that DBA mice provide a model of hippocampal dysfunction. Poor performance of DBA mice in spatial tasks (Ammassari-Teule and Caprioli, 1985) has been correlated with lower neuronal density in the CA1 field (Wimer et al., 1976), a smaller number of mossy-fiber terminals in the hippocampal region inferior (Schwegler and Crusio, 1995), and lower hippocampal protein kinase C activity (Wehner et al., 1990) as compared to C57 mice. We previously showed that DBA mice displayed a similar pattern of deficits as rats with dorsal hippocampal lesions, whereas C57 mice performed like control rats (Ammassari-Teule et al., 1995). A further study (Thinus-Blanc et al., 1996) revealed that a dorsal hippocampal lesion abolished the habituation and reaction to the spatial change in C57 mice, whereas it induced a nonspecific decrease of object exploration in DBA mice. APC lesions did not affect habituation in either group. The lesions were found to abolish the reaction to spatial change in

C57 mice, but they did not affect spatial performance and behavior in DBA mice. The results confirm and extend previous findings (Save et al., 1992) suggesting that in C57 mice, the hippocampus and the APC cooperate in the elaboration and use of a spatial representation through exploratory activity. In contrast, in DBA mice, the hippocampus but not the APC revealed some residual function. This is consistent with the idea that the participation of the APC depends on the degree of functionality of the hippocampus. Interestingly, the opposite pattern of effects was found when DBA and C57 mice with hippocampal and APC lesions were tested in a radial eight-arm maze with all arms baited (Ammassari-Teule et al., 1998). APC lesions induced a more severe impairment in DBA mice than in C57 mice.

The results of the two mice studies suggest that both the hippocampus and APC participate in spatial processing, and that the function of the APC depends on the degree of functionality of the hippocampus. It can also be concluded that the respective contribution of these two structures varies as a function of the task.

Although both the exploratory situation and the radial maze task require the combination of visual and idiothetic information, the complexity of such combination may differ between the two tasks. First, the shape and the structure of the environments used in each task are clearly different, thus providing very different pieces of spatial information to allow self-localization. Second, the exploratory situation requires the use of proximal cues (objects placed in the circular arena), whereas the radial maze task requires the use of distal cues (room cues).

Since the appearance and apparent topological relationship of immediate three-dimensional objects may change considerably when the animal moves across short distances, extracting the spatial invariants using intramaze objects may require more intensive movements between various viewpoints than using distal cues. We therefore assume that elaborating a spatial representation on the basis of intramaze objects involves a more thorough combination of visual and idiothetic information than when based on remote cues. This difference may yield a dissociation of the effects of hippocampal and APC lesions. We recently tested this hypothesis by training hippocampal, APC, and control rats in three successive navigation tasks in the water maze (Save and Poucet, 2000). In the first task (proximal condition, see Fig. 3A), rats had to navigate toward a hidden platform by using intramaze objects (the influence of extramaze cues was neutralized). In the second task (distal condition), rats had to locate the platform by using the room cues. In the third task (beacon condition, see Fig. 3A), a salient beacon was associated with the hidden platform (distal cues were eliminated). Hippocampal rats displayed a deficit in both the proximal and distal conditions (Fig. 3A,B), whereas APC rats were impaired mainly in the proximal condition (Fig. 3A). In contrast, both lesioned groups displayed control-like performance in the beacon condition. Once again, the hippocampus and APC are jointly involved in a task in which combining visual and idiothetic information is made complex (proximal condition). In contrast, the involvement of the APC seems marginal when such associations are simpler (distal condition). This is consistent with a number of studies showing that rats with APC lesions display a moderate deficit in the water maze task with distal cues (Kolb et al., 1983; Kolb and Walkey, 1987; Save and Moghaddam, 1996).

Overall, these behavioral results support the hypothesis that the APC and the hippocampus interact in the processing of visuospatial information provided by the location of cues in space and idiothetic information provided by self-motion. They suggest, in addition, that the APC is mostly involved when building up a spatial representation that requires complex combinations between these two categories of sensory information. This hypothesis is consistent with the results of McNaughton et al. (1989), showing that the activity of some APC cells is selective for combinations of spatial features and specific movements as the animal performs a spatial task in the radial eight-arm maze. For instance, a given cell was active when the animal turned left at the end of a given arm (but not when it turned right or at the center of the maze). In addition, other cells were found to be selective only for specific movements (McNaughton et al., 1994), suggesting that different stages in the combination of visual and idiothetic information are performed within the APC. In the hippocampus, place-cell spatially selective firing depends on cooperation and balance between visuospatial and idiothetic cues (Sharp et al., 1995; Wiener et al., 1995; Bures et al., 1997; Rotenberg and Muller, 1997; Knierim et al., 1998). In addition, when there is a conflict between these two categories of cues, the rat can rely appropriately on one or the other category according to the magnitude of the conflict (Jeffery, 1998).

CONCLUSIONS

Although few studies have directly compared the effects of hippocampal and APC lesions in spatial behaviors, the results are consistent with the view that both structures contribute to the combination of visual and idiothetic information, although the question of their respective functions in such processing and of their interactions remains open. The similarity of the behavioral effects of hippocampal and parietal lesions observed in some studies may reflect a close functional relationship between the hippocampus and the APC. However, one has to envision the more likely interpretation that the hippocampus and the APC play complementary albeit distinct roles. Indeed, the combination of visual and idiothetic information is a fundamental process which is probably distributed over several brain structures with different possible levels of abstraction, and which is necessary for different navigating systems.

As suggested above, one function of the APC might be to associate visual and self-motion sensory inputs at early stages of spatial processing, i.e., when new environmental information has to be processed. This would eventually allow the construction of an allocentric spatial representation in the hippocampus (see also Save et al., 1998 for a previous statement of this hypothesis). As suggested by electrophysiological data, the APC function could encompass several stages, reflecting the progressive combination of visuospatial and self-motion cues, and thus resulting in a multiple and redundant integration between the ever-changing visual scene and the rat's movements across the environment. Basically, the visual and idiothetic inputs to the APC are coded in an egocentric

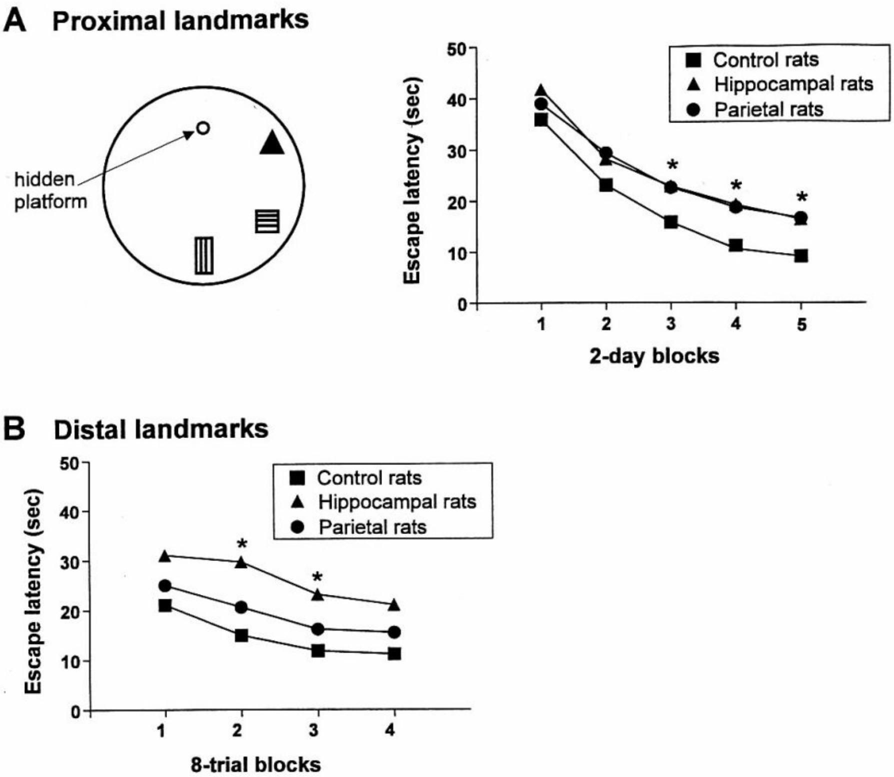

FIGURE 3. A: Proximal landmark condition. Left: View from above of the water maze containing three distinct objects. The apparatus was surrounded by opaque curtains to eliminate distal visual cues, and the set of objects was rotated from one session to another. Right: Mean escape latency across acquisition for control, hippocampal, and APC rats. Asterisks indicate significant differences between the lesioned and control rats. B: Distal landmark condition. The rats were allowed to use room cues to locate the hidden platform. Mean escape latency across acquisition for control, hippocampal, and APC rats. Only hippocampal rats were impaired with respect to control rats. Asterisks indicate significant differences (from Save and Poucet, 2000).

frame of reference. This is supported by the fact that head direction neurons code for head-centered space (Chen and Nakamura, 1998) and that their activation may be determined by the interaction between current head direction and angular movement as estimated on the basis of idiothetic inputs (McNaughton et al., 1991). The assumption that the APC participates in the gradual conversion of egocentrically coded information into allocentrically coded information by combining visuospatial to idiothetic inputs raises a number of issues for further investigations. 1) Is the APC absolutely necessary for the conversion process, or is it only partially involved? The results of lesion studies show that the behavioral performance of rats in allocentric tasks is not systematically affected by APC lesions, suggesting that the APC is involved only in some situations, perhaps when the visual-idiothetic association requirements are very important (Save and Poucet, 2000). 2) To what extent is this conversion performed in the APC? Do some APC cells have allocentric functional correlates? This is a possibility, since recent work has revealed that the activity of some neurons reflects an allocentric component (Chen and Nakamura, 1998). 3) What is the contribution of other structures that are intermediate between the APC and the hippocampus, such as the retrosplenial or entorhinal cortices? Do they participate in this conversion process, or do they have other independent functions? The fact that these structures also probably incorporate some visual or idiothetic information (Cooper and Mizumori, 1999) is compatible with the hypothesis that they contribute to the conversion process initiated at the APC level. The outcome of successive processing via the APC-retrosplenial-entorhinal axis may then reach the hippocampus, where the formation of the allocentric representation is completed. 4) Does the hippocampus have an active role in the transformation of egocentric to allocentric information, or does it only store the outcome of upstream processes? 5) Does the hippocampus exert a control, even indirect, on APC function? This hypothesis is suggested by neuroanatomical data showing that the APC and the hippocampus, via intermediate structures, are interconnected.

To date, the study of the functional relationship between the APC and the hippocampus is only at its beginning. We need not only to improve our knowledge of the role of the APC, but also to uncover the contribution of other structures belonging to this functional network. In addition, we must take into account the mnemonic and attentional aspects involved in spatial processing. Finally, the investigation of the hippocampal-parietal relationship may provide some basic theoretical elements in common with other functional interactions between subcortical and cortical structures, and between functional networks in the brain.

REFERENCES

Alyan SH, McNaughton BL. 1999. Hippocampectomized rats are capable of homing by path integration. Behav Neurosci 113:19–31.

Ammassari-Teule M, Caprioli A. 1985. Spatial learning and memory, maze running strategies and cholinergic mechanisms in two inbred strains of mice. Behav Brain Res 17:9–16.

Ammassari-Teule M, Tozzi A, Rossi-Arnaud C, Save E, Thinus-Blanc C. 1995. Reactions to spatial and non spatial change in two inbred strains of mice: further evidence supporting the hippocampal dysfunction hypothesis in the DBA/2 strain. Psychobiology 23:284–289.

Ammassari-Teule M, Save E, de Marsanich B, Thinus-Blanc C. 1998. Posterior parietal cortex lesions severely disrupt spatial learning performance in the DBA strain characterized by a genetic hippocampal dysfunction. Behav Brain Res 95:85–90.

Andersen RA, Essick GK, Siegel RM. 1985. Encoding of spatial location by posterior parietal neurons. Science 230:456–458.

Blair HT, Sharp PE. 1996. Visual and vestibular influences on head-direction cells in the anterior thalamus of the rat. Behav Neurosci 110:643–660.

Blair TH, Lipscomb BW, Sharp PE. 1997. Anticipatory time intervals of head direction cells in the anterior thalamus of the rats: implications for path integration in the head-direction circuit. J Neurophysiol 78: 145–159.

Bures J, Fenton AA, Kaminskij Y, Rossier J, Sachetti B, Zinyuk L. 1997. Dissociation of exteroceptive and idiothetic orientation cues: effect on hippocampal place cells and place navigation. Philos Trans R Soc Lond [Biol] 352:1515–1524.

Boyd MG, Thomas RK. 1977. Posterior association cortex lesion in rats: mazes patterns discrimination, and reversal learning. Physiol Psychol 4:455–461.

Chandler HC, King V, Corwin JV, Reep RL. 1992. Thalamocortical connections of rat posterior parietal cortex. Neurosci Lett 143:237–242.

Chen LL, Nakamura K. 1998. Head-centered representation and spatial memory in rat posterior parietal cortex. Psychobiology 26:119–127.

Chen LL, Lin LH, Green EJ, Barnes CA, McNaughton BL. 1994a. Head-direction cells in the rat posterior cortex. I. Anatomical distribution and behavioral modulation. Exp Brain Res 101:8–23.

Chen LL, Lin LH, Barnes CA, McNaughton BL. 1994b. Head-direction cells in the rat posterior cortex. II. Contribution of visual and idiothetic information to the directional firing. Exp Brain Res 101:24–34.

Cooper BG , Mizumori SJY. 1999. Retrosplenial cortex inactivation selectively impairs navigation in darkness. Neuroreport 1:625–630.

Corwin JV, Reep RL. 1998. Rodent posterior parietal cortex as a component of a cortical network mediating directed spatial attention. Psychobiology 26:87–102.

Davis BK, McDaniel WF. 1993. Visual memory and visual spatial functions in the rat following parietal and temporal cortex injuries. Physiol Behav 53:145–151.

DeCoteau WE, Kesner RP. 1998. Effects of hippocampal and parietal cortex lesions on the processing of multiple-object scenes. Behav Neurosci 112:68–82.

Etienne A, Maurer R, Séguinot V. 1996. Path integration in mammals and its interaction with visual landmarks. J Exp Biol 199:201–209.

Fukushima K. 1997. Corticovestibular interactions: anatomy, electrophysiology, and functional considerations. Exp Brain Res 117:1–16.

Golob EJ, Taube JS. 1999. Head direction cells in rats with hippocampal or overlying neocortical lesions: evidence for impaired angular path integration. J Neurosci 19:7198–7211.

Guldin W, Mirring S, Grüsser O-J. 1992. Monosynaptic input from the cerebral cortex to the vestibular brainstem nuclei in the rat. Soc Neurosci Abstr 19:510.

Guldin W, Mirring S, Grüsser O-J. 1993. Connections from the neocortex to the vestibular brain stem nuclei in the common marmoset. Neuroreport 5:113–116.

Jeffery KJ. 1998. Learning of landmark stability and instability by hippocampal place cells. Neuropharmacology 37:677–687.

Kawano K, Sasaki M, Yamashita M. 1980. Vestibular input to visual tracking neurons in the posterior parietal cortex of the monkey. Neurosci Lett 17:55–60 .

Knierim JJ, Kudrimoti HS, McNaughton BL. 1998. Interactions between idiothetic cues and external landmarks in the control of place cells and head direction cells. J Neurophysiol 80:425–446.

Kolb B. 1990. Association cortex in the rat. In: Kolb B, Tees RC, editors. The cerebral cortex of the rat. Cambridge, MA: MIT Press. p 433–471.

Kolb B, Walkey J. 1987. Behavioural and anatomical studies of the posterior parietal cortex in the rat. Behav Brain Res 23:127–145.

Kolb B, Sutherland RJ, Whishaw IQ. 1983. A comparison of the contributions of frontal and parietal association cortex to spatial localization in rats. Behav Neurosci 97:13–27.

Kolb B, Buhrmann K, McDonald R, Sutherland RJ. 1994. Dissociation of the medial prefrontal, posterior parietal, and posterior temporal cortex for spatial navigation and recognition memory in the rat. Cereb Cortex 6:664–680.

Krieg WJS. 1946. Connections of the cerebral cortex: I. The albino rat: A. Topography of the cortical areas. J Comp Neurol 84:221–275.

Long JM, Kesner RP. 1996. The effects of dorsal versus ventral hippocampal, total hippocampal, and parietal cortex lesions on memory for allocentric distance in rats. Behav Neurosci 110:922–932.

Long JM, Kesner RP. 1998. Effects of hippocampal and parietal cortex lesions on memory for egocentric distance and spatial location information in rats. Behav Neurosci 112:480–495.

Lynch JC. 1980. The functional organization of the posterior parietal cortex. Behav Brain Sci 3:485–499.

Markus EJ, Barnes CA, McNaughton BL, Gladden VL, Skaggs WE. 1994. Spatial information content and reliability of hippocampal CA1 neurons: effects of visual input. Hippocampus 4:410–421.

McDaniel WF, Skeel RL. 1993. Visual-spatial function persist following temporal and posterior parietal cortex lesions in the rat. Physiol Behav 53:199–203.

McDaniel WF, McDaniel SE, Thomas RK. 1978. Thalamocortical projections to the temporal and parietal association cortices in the rat. Neurosci Lett 7:121–125.

McDaniel WF, Wildman LD, Spears RH. 1979. Posterior association cortex and visual pattern discrimination in the rat. Physiol Psychol 7:241–244.

McDaniel WF, Via JD, Smith JS, Wells DL, Fu JJ, Bishop JF, Boyd PA, Lesdesma HM. 1995. Unilateral injury of posterior parietal cortex and spatial leaning in hooded rats. Behav Brain Res 70:165–179.

McNaughton BL, Leonard B, Chen L. 1989. Cortical-hippocampal interactions and cognitive mapping: a hypothesis based on reintegration of the parietal and inferotemporal pathways for visual processing. Psychobiology 17:230–235.

McNaughton BL, Chen LL, Markus EJ. 1991. "Dead reckoning," landmark learning, and the sense of direction: a neurophysiological and computational hypothesis. J Cogn Neurosci 3:190–202.

McNaughton BL, Mizumori SJY, Barnes CA, Leonard BJ, Marquis M, Green EJ. 1994. Cortical representation of motion during unrestrained spatial navigation in the rat. Cereb Cortex 4:27–39.

Meunier M, Jaffard R, Destrade C. 1991. Differential involvement of anterior and posterior cingulate cortices in spatial discriminative learning in a T-maze in mice. Behav Brain Res 44:133–143.

Muller RU. 1996. A quarter of a century of place cells. Neuron 17:813–822.

O'Keefe J, Nadel N. 1978. The hippocampus as a cognitive map. Oxford: Clarendon Press.

Poucet B. 1993. Spatial cognitive maps in animals: new hypothesis on their structures and mechanisms. Psychol Rev 100:163–182.

Reep RL, Chandler HC, King V, Corwin JV. 1994. Rat posterior parietal cortex: topography of cortical and thalamic connections. Exp Brain Res 100:67–84.

Rotenberg A, Muller RU. 1997. Variable coupling to a continuous viewed stimulus: evidence that the hippocampus acts as a perceptual system. Philos Trans R Soc Lond [Biol] 352:1505–1513.

Qin YL, McNaughton BL, Skaggs WE, Barnes CA. 1997. Memory reprocessing in corticocortical and hippocampocortical neuronal ensembles. Philos Trans R Soc Lond [Biol] 352:1525–1534.

Save E, Moghaddam M. 1996. Effects of lesions of the associative parietal cortex in the acquisition and use of spatial memory in egocentric and allocentric navigation tasks in the rat. Behav Neurosci 110:74–85.

Save E, Poucet B. 2000. Involvement of the hippocampus and associative parietal cortex in the use of proximal and distal landmarks for navigation. Behav Brain Res 109:195–206.

Save E, Poucet B, Foreman N, Buhot M-C. 1992. Objects exploration and reaction to a spatial and a non-spatial change in the rat following damage to the posterior parietal cortex or the dorsal hippocampus. Behav Neurosci 106:447–456.

Save E, Poucet B, Foreman N, Thinus-Blanc C. 1998. The contribution of the associative parietal cortex and hippocampus to spatial processing in rodents. Psychobiology 26:153–161.

Sharp PE, Blair HT, Etkin D, Tzanetos DBJ. 1995. Influences of vestibular and visual motion information on the spatial firing patterns of hippocampal place cells. J Neurosci 15:173–189.

Schwegler H, Crusio WE. 1995. Correlations between radial maze learning and structural variations of septum and hippocampus in rodents. Behav Brain Res 67:29–41.

Smith PF. 1997. Vestibular-hippocampal interactions. Hippocampus 7:465–471.

Sutherland RJ, Whishaw IQ, Kolb B. 1988. Contributions of cingulate cortex to two forms of spatial learning and memory. J Neurosci 8:1863–1872.

Taube JS, Goodridge JP, Golob EJ, Dudchenko PA, Stackman RW. 1996. Processing the head direction cell signal: a review and commentary. Brain Res Bull 40:477–486.

Thinus-Blanc C, Save E, Rossi-Arnaud C, Tozzi A, Ammassari-Teule M. 1996. The difference shown by C57BL/6 and DBA/2 inbred mice in detecting spatial novelty are subserved by a different hippocampal and parietal cortex interplay. Behav Brain Res 80:33–40.

Thomas RK, Weir VK. 1975. The effects of lesions in the frontal or posterior association cortex of rats on maze III. Physiol Psychol 3:210–214.

Ungerleider LG, Mishkin M. 1982. Two cortical visual systems. In: Ingle DJ, Goodale MA, Wansfield RJ, editors. Analysis of visual behavior. Cambridge, MA: MIT Press. p 549–586.

Wehner JM, Sleight S, Upchurch M. 1990. Hippocampal protein kinase C is reduced in poor spatial learners. Brain Res 523:181–187.

Whishaw IQ, Maaswinkel H. 1998. Rats with fimbria-fornix lesions are impaired in path integration: a role for the hippocampus in "sense of direction." J Neurosci 18:3050–3058.

Whishaw IQ, Tomie J. 1997. Piloting and dead reckoning dissociated by fimbria-fornix lesions in a rat food carrying task. Behav Brain Res 89:97–98.

Wiener SI, Korshunov VA, Garcia R, Berthoz A. 1995. Inertial, substratal and landmark cue control of hippcoampal CA1 place cell activity. Eur J Neurosci 7:2206–2219.

Wimer RE, Wimer CC, Vaugh JE, Barber RP, Balvanz BA, Chernow CR. 1976. The genetic organization of neuron number in Ammon's horns of house mouse. Brain Res 118:219–243.

Witter MP. 1993. Organization of the entorhinal-hippocampal system: a review of current anatomical data. Hippocampus 3:33–44.

Wyss JM, van Groen T. 1992. Connections between the retrosplenial cortex and the hippocampal formation in the rat: a review. Hippocampus 2:1–12.

Zilles K. 1985. The cortex of the rat: a stereotaxic atlas. Berlin: Springer-Verlag.