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Role of the parietal cortex in long-term representation of spatial information in the rat

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ABSTRACT

The processing of spatial information in the brain requires a network of structures within which the hippocampus plays a prominent role by elaborating an allocentric representation of space. The parietal cortex has long been suggested to have a complementary function. An overview of lesion and unit recording data in the rat indicates that the parietal cortex is involved in different aspects of spatial information processing including allocentric and egocentric processing. More specifically, the data suggest that the parietal cortex plays a fundamental role in combining visual and motion information, a process that would be important for an egocentric-to-allocentric transformation process. Furthermore, the parietal cortex may also have a role in the long-term storage of representation although this possibility needs further evidence. The data overall show that the parietal cortex occupies a unique position in the brain at the interface of perception and representation.

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1. Introduction

Spatial behaviors are essential to survival of most animal species. Evolution yielded the emergence of spatial strategies that allow animals to maintain their navigational capability and their spatial memory in spite of environmental modifications. Understanding how the brain processes spatial information has motivated a huge amount of work. It is now well established that the processing of spatial information in the brain requires a network of cortical and subcortical structures within which the hippocampus plays a central role by implementing an allocentric representation of space. One of the most striking evidence in favor of such a role comes from the existence in CA1 and CA3 of pyramidal neurons characterized by location-specific firing, the so-called place cells (O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978). The discovery of place cells in the 1970s has had a great conceptual influence and contributed to promote a "hippocampus-centered" view of the processing of spatial information in the brain. However, that a phylogenetically preserved, paleocortical structure such as the hippocampus could be the neural substrate of high level cognitive processes implicitly raised the question of the role of the neocortex in rodents. In this respect, the influence of Lashley's theories was still perceptible in the 1970s (McDaniel, Wildman, & Spears, 1979; Thomas, 1970; Thomas & Weir, 1975). As the main proponent of a holistic view of cortical functions in learning twenty years before, Lashley had postulated that cortical areas do not have spe-

cific functions as far as learning is concerned and can substitute for each other when a lesion is made (equipotentiality principle). Several decades later, this theory motivated studies that examined the effects of lesioning various parts of the cortex on learning performance. Lesions of the posterior association cortex, frontal cortex and temporal cortex produced different effects on various learning tasks thus questioning Lashley's equipotentiality principle and perhaps more importantly, suggesting a specific contribution of the posterior association cortex (McDaniel & Thomas, 1978; Thomas, 1970; Thomas & Weir, 1975). In the context of a strong disagreement in the literature regarding the existence of a posterior association cortex in the rat, these seminal studies are among the first to propose that this region has a distinct role in spatial learning and memory. This renewal of interest for the parietal cortex in the rat produced a large number of studies that sought to characterize this cortical area both neuroanatomically and functionally. The results provide a great deal of evidence in favor of a role in the formation of long-term spatial representations. This aim of this review is to summarize this evidence and to suggest possible directions for further work.

2. The parietal cortex is involved in multimodal processing: Anatomical evidence

The hypothesis of the existence of a posterior association cortex (hereafter referred to as parietal cortex) in the rat has been initially founded on neuroanatomical bases. Using cytoarchitectonic characteristics, Krieg described a parietal region subdivided into six areas (Krieg, 1946), three primary somatosensory areas (labeled

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1, 2, 3 according to Brodmann's nomenclature) and three areas putatively involved in multisensory integration (labeled 7, 39, 40). Subsequently, Krieg's area 7 was considered as corresponding to the parietal cortex by Kolb and Walkey (1987). This area, lying between the rostral primary somatosensory areas and the caudal secondary visual areas, would differ from the neighboring regions by a reduction in layer thickness and fewer fibers (Kolb, 1990). The parietal cortex was also described on the basis of its thalamic inputs. Authors agreed that the thalamic projections to the parietal cortex originated from the lateroposterior and laterodorsal nuclei (Chandler, King, Corwin, & Reep, 1992; Kolb & Walkey, 1987; Lashley, 1941; McDaniel, McDaniel, & Thomas, 1978; Reep, Chandler, King, & Corwin, 1994). However, such connections are not specific since the lateroposterior nucleus also has extensive projections to various cortical areas including primary and secondary visual cortex, medial prefrontal and anterior cingulate cortex (Musil & Olson, 1988a, 1988b) and subcortical regions such as the striatum (Kamishina, Yurcisin, Corwin, & Reep, 2008). Whether there is topographic organization of the neurons within the lateroposterior thalamus with respect to their cortical site of projection is not clearly established. Most importantly, strong support for the hypothesis of an associative function in the parietal cortex is provided by the pattern of corticocortical connections. As shown in Fig. 1, the parietal cortex receives inputs from various sensory regions including the somatosensory cortex (Par 1 according to Zilles' nomenclature, Zilles, 1985), primary and secondary visual cortex (Oc1, Oc2L, Oc2M), and the auditory cortex (Te1) (Kimura, Donishi, Okamoto, & Tamai, 2004; Kolb, 1990; Kolb & Walkey, 1987; Miller & Vogt, 1984; Reep et al., 1994; Torrealba, Olavarria, & Carrasco, 1984). It is also connected to cortical regions involved in goal-directed behavior such as the orbitofrontal, and medial prefrontal cortices (LO, VLO, Fr2) (Kolb & Walkey, 1987; Nelson, Sarter, & Bruno, 2005; Reep et al., 1994). Interestingly, the parietal cortex receives inputs from the cerebellum suggesting a direct link with motor systems (Giannetti & Molinari, 2002). It may also have some connection with the vestibular system either monosynaptically (Guldin, Mirring, & Grüsser, 1992) or polysynaptically via the lateroposterior thalamic nucleus (Smith et al., 2005) but this remains to be clarified. Consistent with the hypothesis of a role in spatial memory, the parietal cortex is connected to the limbic system and in particular to the hippocampal formation via the retrosplenial and the postrhinal cortex (Burwell & Amaral, 1998). Note how-

ever that nothing is known about the topographical organization of the projections within the parietal cortex. One can assume that the projections are not intermingled over the whole parietal surface but on the contrary segregated but this hypothesis remains to be confirmed. Overall, this complex pattern of connection strongly suggests that the parietal cortex is part of various networks involved in the processing of sensory, motor information and in memory. It therefore may play a unique role in multimodal processing and, as a result, would be an important actor in many cognitive processes in the rat.

3. Effects of parietal cortex lesions in the processing of allocentric information

Parietal cortex lesion studies were performed not only to uncover the role of this structure in spatial learning but also to discriminate it from that of the hippocampus. The possibility that the cognitive map or at least an elementary form was elaborated in the parietal cortex before being fully realized in the hippocampus was raised. To investigate the contribution of the parietal cortex in long-term representation of spatial information, a number of studies examined the effects of parietal lesions in place navigation tasks that involve the formation and use of an allocentric spatial representation. Most of these studies used the Morris water maze but a few used alternative situations such as the cheese board task, a dry version of the water maze (Kesner, Berman, & Tardif, 1992). In the Morris water maze, the animals are required to locate a submerged platform by using a configuration of environmental cues. Lesions yielded variable effects. Rats with parietal cortex lesions were at best non affected (Compton, Griffith, McDaniel, Foster, & Davis, 1997; Kolb, Sutherland, & Whishaw, 1983; Save & Poucet, 2000a) and at worst mildly impaired in the acquisition of this task (Kolb, Burhmann, McDonald, & Sutherland, 1994; Kolb, Holmes, & Whishaw, 1987; Kolb & Walkey, 1987; Save & Moghaddam, 1996). In contrast, a marked deficit was found by DiMattia and Kesner (1988) and Hoh and co-workers (2003). However, in the DiMattia and Kesner study, it is possible that the deficits would result from larger lesion size and more anterior lesion location than the other studies. We also showed that the parietal cortex is not recruited when the hippocampus is inactivated during place learning (Paron, Poucet, & Save, 2001). Using a distributed learning procedure, we found that short-lasting reversible inactivation of the dorsal

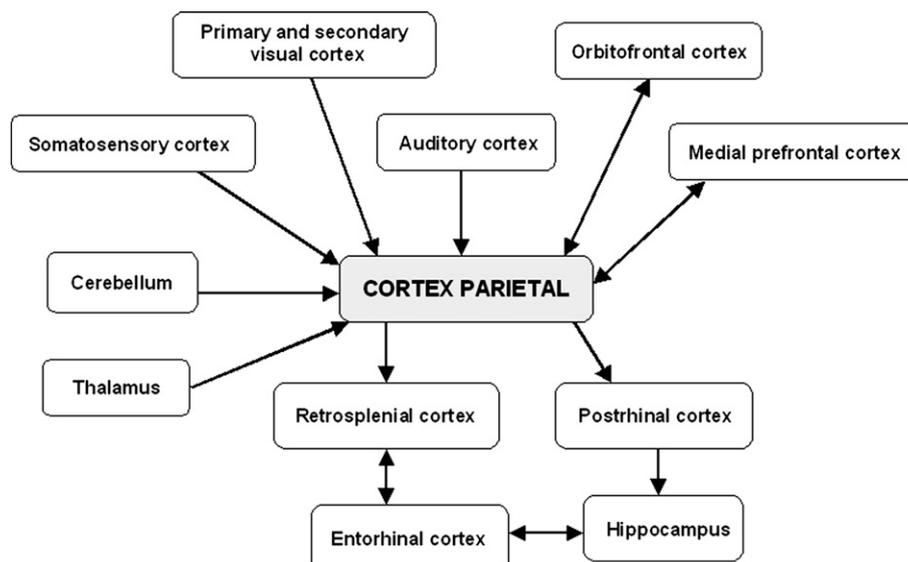


Fig. 1. Main cortical and subcortical connections of the parietal cortex in the rat.

hippocampus during the navigation trials in the Morris water maze did not prevent learning of a platform location, therefore suggesting the involvement of another structure for acquisition, storage and off line processing. The possibility that this structure could be the parietal cortex was ruled out since rats with parietal cortex lesions that had their hippocampus inactivated were able to perform the task as well as rats with just an inactivated hippocampus. Thus, the parietal cortex does not appear to be the brain area that compensates for a dysfunctioning hippocampus. As a whole, the results suggest that the parietal cortex plays a role in the formation of spatial representations but this role appears to be not critical for place learning and navigation.

That hippocampal lesions had much more deleterious effects on place navigation than parietal cortex lesions (e.g. Compton et al., 1997; Morris Garrud, Rawlins, & O'Keefe, 1982) suggested that these two regions contribute to different aspects of the processing of spatial information. Interestingly, Kolb and colleagues observed that rats with parietal cortex lesions were able to learn the general location of the platform by using room cues but had difficulties in adjusting their movement toward the goal (Kolb et al., 1994; Kolb & Walkey, 1987). Because this deficit did not appear when the animals had to navigate toward a visible goal, the possibility of a pure motor impairment is unlikely. A more appealing hypothesis would consider the possibility that the parietal lesion is involved in the conjoint integration of spatial features and motion information, a process that may be important for the formation of the hippocampal cognitive map (McNaughton, Leonard, & Chen, 1989; McNaughton et al., 1994). A study in which rats were trained to navigate to a submerged platform with cues/objects directly placed in the pool provided results consistent with this hypothesis. This study was based on the assumption that building an allocentric representation requires extraction of spatial invariants in the environment. It has been proposed that this process involves conjoint integration of different views of the environment with movements connecting these views (Poucet, 1993; Poucet & Benhamou, 1997). Because of parallax effects, using intramaze cues may require enhanced association between views and motion to form a spatial representation. Rats with parietal cortex lesions were impaired when they had to use intramaze cues but not when they had to use distant cues whereas rats with hippocampal lesions were impaired regardless the kind of cues they used (Save & Poucet, 2000a). The notion that the parietal cortex cooperates with the hippocampus and is involved in the formation of spatial representations based on proximal objects is further supported by a study that examined the effects of parietal lesions on hippocampal place activity. Place cells were recorded in parietal-lesioned rats as the animals performed a pellet chasing task in a circular arena containing three objects (Save, Paz-Villagrán, Alexinsky, & Poucet, 2005). Room cues were made irrelevant by placing a curtain around the arena. We found that place field stability was perfectly controlled by the intramaze objects in control rats. Ninety degree rotation of the set of objects in the absence of the rat resulted in equivalent rotation of the place fields. In contrast, in parietal-lesioned rats, the control of place fields by the objects was much weaker since a majority of fields did not rotate but remained stable relative to the room reference frame. We also examined whether the rats could use olfactory and idiothetic cues to maintain stable fields by removing the objects. This was the case for control rats in which place fields remained stable. In contrast, place fields in lesioned rats shifted to their initial position, suggesting that place cells did not use combined olfactory and idiothetic cues but background cues to maintain stable fields (see Fig. 2). We assumed that because parietal-lesioned rats were unable to properly use proximal objects, place cells eventually used non controlled cues. If this hypothesis is correct, then place cell activity in parietal-lesioned rats should be normally controlled by distal cues. Beyond this

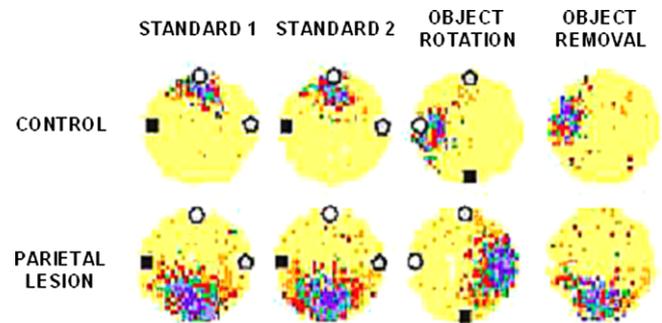


Fig. 2. Examples of firing rate maps of two hippocampal place cells recorded in four successive sessions in control and parietal-lesioned rats. Rats were foraging in a circular arena containing three objects (represented as a black square, white circle, and white polygon). Dark pixels indicate the place field of the cell. In control rats, place field were controlled by the objects, i.e. rotated an equivalent amount after object rotation, and remained stable after object removal suggesting a control by non visual (e.g. idiothetic, olfactory) cues. In contrast, in parietal-lesioned rats, a number of place fields were not controlled by the objects (not illustrated). In addition, after object removal, place fields shifted back to their initial location (Standard 1/Standard 2).

assumption, this study is a demonstration that the parietal and the hippocampus are functionally related in spite of indirect neuro-anatomical relationships.

As a whole, the data are compatible with the idea that the parietal cortex plays a role in the combination of visuo-spatial and motion information but also provide some new hints on the organization of cue encoding processes. Proximal cues, i.e. objects placed in the animal's locomotor space, and distal cues, i.e. room cues, may be differentially encoded by different structures in the brain. These results and others suggest that the parietal cortex is preferentially involved in the processing of proximal cues whereas the entorhinal cortex is preferentially involved in the processing of distal cues. The hippocampal system would have a major role in combining the two kinds of information to form an integrated spatial representation (Parron, Poucet, & Save, 2004; Save & Poucet, 2000a; Van Cauter, Poucet, & Save, 2008).

The effects of parietal cortex lesions were also examined in non-associative tasks. Save and colleagues used a habituation/dishabituation situation in which the rats explored an arena containing several objects (Save, Poucet, Foreman, & Buhot, 1992). The objects formed a particular configuration that remained constant during the habituation sessions but was modified during the spatial change and non-spatial change sessions. It is important to note that each animal was run only one time and that the whole sequence of session was completed in approximately 1 h. When repeatedly exposed to the initial configuration, both sham-operated and parietal-lesioned rats exhibited habituation, i.e. a decrease of object exploration and locomotor activity. It was assumed that rats would form a spatial representation during habituation. To test this hypothesis, the effects of changing the spatial configuration were examined by displacing some objects. Such a manipulation induced a renewal of exploration specifically directed toward the displaced objects in sham-operated rats. In contrast, rats with parietal lesions did not display such a renewal, suggesting that they were impaired in elaborating a spatial representation on the basis of the object configuration. In addition it was demonstrated that this deficit is specific of manipulation of spatial relationships since a non-spatial change (replacing a familiar object with a novel object) induced a renewal of exploration in the two groups. In this situation, rats with hippocampal lesions displayed similar pattern of performance as rats with parietal lesions: they were impaired in the detection of spatial but not non-spatial change. At this point, the comparison of the impact of parietal

lesions in associative and non-associative tasks is instructive. First, the parietal cortex seems to play a greater role when the animal has to use a configuration of intramaze objects than a configuration of extramaze cues to form a spatial representation. This supports the hypothesis that the parietal cortex is involved in the association between visuo-spatial and motion-related information. Second, the contribution of the parietal cortex would be fully revealed when encoding of spatial information is performed within a limited amount of time that does not allow for compensatory processes and/or neural activation. Such processes may account for the reduced deficits when training is distributed over days.

Both the parietal cortex and the hippocampus are involved in the processing of complex spatial information but their specific contributions remain unclear. In the perspective of disentangling their respective roles, studies compared the effects of parietal cortex and hippocampal lesions in various spatial tasks. In a scene discrimination task, both rats with parietal lesions and hippocampal lesions exhibited impaired detection of spatial and spatial/object changes but not object changes (DeCoteau & Kesner, 1998), an effect in line with Save et al.'s findings (1992). Later it was suggested that this effect could result from the inability of parietal-lesioned rats to process topological information and of hippocampal-lesioned rats to process metric information (Goodrich-Hunsaker, Howard, Hunsaker, & Kesner, 2008; Goodrich-Hunsaker, Hunsaker, & Kesner, 2005). In contrast, neither the parietal cortex nor the hippocampus seem to be involved in the discrimination of spatial location or allocentric distance as measured in a delayed-matching-to-sample go/no go task (Long & Kesner, 1996, 1998). However, the parietal cortex would play a weaker role in the memory for allocentric distance than the hippocampus in a similar paradigm (Long & Kesner, 1996). Rats with parietal lesions were not impaired in learning an allocentric version of a Hebb-Williams maze but were impaired in an egocentric version. Rats with hippocampal lesions were impaired in the allocentric but not egocentric version (Rogers & Kesner, 2006). These results do not provide a clear picture of the respective roles of the parietal cortex, hippocampus, and parietal-hippocampal relationships. They nevertheless suggest that the parietal cortex has a more subtle role in spatial representation than the hippocampus. In particular, parietal lesions appeared to affect or spare the ability to process and memorize spatial information depending on the experimental set up and task used. Thus, a possible explanation for these inconsistent effects is that the involvement of the parietal cortex and therefore of the parietal-hippocampal interaction would be highly dependent on the cognitive demand, task contingencies, and behavioral constraints. This hypothesis is supported by the results of a recent study in which Rogers and Kesner used a disconnection procedure to more directly examine the importance of cortical-hippocampal interaction in the processing of spatial information (Rogers & Kesner, 2007). In this procedure, the rats received unilateral lesions in both the hippocampus and the parietal cortex either on ipsilateral or contralateral hemisphere. If the two structures interact, contralateral lesions are expected to completely disrupt the parietal-hippocampal relationships therefore producing profound deficits whereas ipsilateral lesions that partially damage the relationships would produce only mild deficits. Rats were trained in different spatial tasks including an object-place paired associate learning task, a dry-land place navigation task and a reaction-to-change task. Rats with contralateral lesions were more impaired than rats with ipsilateral lesions in the object-place learning task and the dry-land task. In contrast, both groups were similarly impaired in the reaction-to change task. Although all three tasks have been shown to be sensitive to both parietal cortex lesions and hippocampal lesions, the results suggest that the parietal cortex and the hippocampus cooperate in the object-place and dry-land navigation task but not in the reaction-to change task. As pointed out

by the authors one possible explanation is that parietal-hippocampal interaction would be important in spatial tasks that induce a gradual (over days) formation of a spatial representation. On the contrary, rapid acquisition of environmental information during exploration involves both the parietal cortex and the hippocampus but do not require an interaction between these two structures. Interestingly, in a recent study using similar disconnection procedure and equivalent tasks, we looked at the interaction between the entorhinal cortex and the hippocampus (Parron, Poucet, & Save, 2006) and obtained opposite effects suggesting entorhinal-hippocampal interactions in the reaction-to-change task but not in the place navigation task. This suggests that formation of a representation and detection of a spatial change during object exploration requires cooperation between the entorhinal cortex and the hippocampus but not between the parietal cortex and the hippocampus. This outcome is consistent with the notion that the cortical-hippocampal interactions are modulated by the task requirements.

4. Effects of parietal cortex lesions in the processing of egocentric information

As in allocentric tasks, parietal cortex lesions produced variable effects in egocentric tasks. Once again, the diversity of the tasks used may account for such inconsistency. Actually, egocentric tasks include a heterogeneous amount of behavioral situations ranging from visually guided navigation in the water maze to path integration in an arena. Thus, these tasks involve different sensory inputs and processes that may be mediated by different brain structures. It not surprising therefore that parietal cortex lesions do not disrupt all egocentric learning tasks. Parietal cortex lesions did not impair navigation to a visible platform in the water maze (Kolb & Walkey, 1987; Save & Poucet, 2000a), learning of an egocentric version of the radial maze (Kesner, Farnsworth, & DiMattia, 1989; Kolb et al., 1994). Memory for egocentric distance in a delayed-matching-to-sample go/no go task was not affected (Long & Kesner, 1998). In contrast, deficits were found in acquisition of a response-learning task in a greek cross-shaped water maze (McDaniel et al., 1995) and route learning task in a Hebb-Williams maze (Rogers & Kesner, 2006).

Few studies were conducted to investigate the possibility that the parietal cortex is involved in the processing of motion information. Generally, in these studies, allothetic cues are removed or made inconsistent in order to encourage the use of idiothetic cues by the animals. For example, Save and Moghaddam (1996) trained rats to reach a platform in the water maze from a fixed start position in total darkness. Lesioning the parietal cortex resulted in inaccurate trajectories so that lesioned rats could not learn the task. Consistent with these results, parietal lesions had a deleterious effect in rats that were trained by using a disorientation procedure to neglect allocentric cues and to rely on egocentric cues to navigate to the platform (Commins, Gemmel, Anderson, Gigg, & O'Mara, 1999). The hypothesis that the parietal cortex is involved in the processing of idiothetic information was further investigated in studies that examined the rats' capability to navigate by path integration. Rats were trained to perform a homing task in a large circular arena. They had to climb on the arena, explore it to find a piece of food hidden in one of 17 food wells and carry the food back, straight to the home cage. Because distant visual cues, directional auditory cues and local olfactory cues were made not relevant, it was assumed that the animals would rely on path integration to return to their home cage. Rats with parietal lesions made more errors, i.e. did not exhibit a correct return, suggesting a path integration deficit. Note that both hippocampal lesions and entorhinal cortex lesions also produced an impairment in this task

(Parron & Save, 2004; Save, Guazzelli, & Poucet, 2001). However, unlike parietal and entorhinal cortex-lesioned rats, hippocampal-lesioned rats exhibited slower acquisition of the basic requirements for the task that may reflect a more general learning impairment. Together, these results suggest that the parietal cortex plays an important role in path integration and that path integration is dependent on the recruitment of a large functional network including at least the parietal cortex, the entorhinal cortex and the hippocampus.

5. Acquisition vs. retention: A role in memory storage?

There is a large consensus that a dialog between the neocortex and the hippocampus is essential for the formation of long-term memory (McClelland, McNaughton, & O'Reilly, 1995). The hippocampus would be necessary for rapid acquisition of new information and short term storage whereas the neocortex would be involved in the storage of remote memories (Frankland & Bontempi, 2005). The parietal cortex has been hypothesized to be activated during consolidation (Maviel, Durkin, Menzaghi, & Bontempi, 2004). Accordingly, post acquisition parietal cortex lesions should affect retention in spatial tasks. This aspect of parietal functioning has been poorly investigated, most studies reporting the effects of lesions made before learning. Among the studies that addressed the acquisition vs. retention issue, Cho and Kesner showed that rats with parietal cortex lesions did not interfere with the retention of two previously learned spatial discriminations in the radial maze. In addition, lesioned rats were able to relearn new discriminations (Cho, Kesner, & Brodale, 1995). In a subsequent study using a similar task, the same authors found a non-temporally graded retention deficit in rats with parietal lesions (Cho & Kesner, 1996). Post acquisition lesions affected the retention of an egocentric navigation task in the water maze and produced a transient deficit in the place navigation (allocentric) version of the task (Commins, Gemmel, Anderson, Gigg, & O'Mara, 1999; Save & Moghaddam, 1996). Hoh et al. (2003) did not find any retention deficit in the place navigation task. Parietal-lesioned rats were found to be impaired in both acquisition and retention of allocentric and egocentric maze learning using the Hebb-Williams maze (Rogers & Kesner, 2006). Thus, in tasks that yielded no or mild acquisition deficits such as the place navigation task in the water maze, parietal lesions were not found to significantly impair retention. In contrast, in tasks that yield acquisition deficits such as egocentric navigation in darkness or route learning in the Hebb-Williams maze, parietal lesions produced retention deficits. Clearly, more data are needed but those available suggest that when the parietal cortex is necessary, it is involved in both initial acquisition and long-term storage of spatial information.

6. Neural activity in the parietal cortex: Unit recordings

Only a very few studies have managed to record unit activity in the parietal cortex in the rat. McNaughton and collaborators recorded parietal neurons as the rats performed a radial maze task. They found that a substantial number of cells exhibited movement correlates, discriminating between right turns, left turns and forward motion. Interestingly, there were cells that appeared to be modulated by a combination of motion and spatial correlates. For examples, some cells were preferentially activated for outwardly directed forward motion (McNaughton et al., 1994). Other cells fired selectively during specific turns at the end but not at the center of the maze. Still more selective spatial correlates were found since there were cells that fired during specific turns in circumscribed parts of the maze, for example in the western arms (McNaughton et al., 1989). Thus, the parietal cortex contains cells

that have correlates ranging from pure motion to conjunctions of motion and spatial correlates.

Further investigations allowed to identify a small number of cells in the parietal cortex that had head direction firing properties (Chen, Lin, Barnes, & McNaughton, 1994b; Chen, Lin, Green, Barnes, & McNaughton, 1994a). Similar cells were also found in the retrosplenial cortex (see also Cho & Sharp, 2001). Some cells exhibited behavioral modulations in addition to their direction-specific firing. For example, there were head direction neurons that were more active for specific movements, e. g. right turns. Head direction-specific firing of parietal neurons was shown to be controlled by environmental and idiothetic cues (Chen et al., 1994b). Some of these neurons showed activity modulation in response to vestibular stimulation (Chen & Nakamura, 1998). This is consistent with the properties of head direction cells recorded in other regions of the brain (Taube, 1998, for a review) and suggests that parietal neurons incorporate information from both environmental cues and movement-related cues including motor and vestibular cues.

Pursuing the idea that parietal neurons encode motion information, Nitz recorded parietal neurons as rats ran along a familiar path in a complex maze including one right and one left turns (Nitz, 2006). He found that parietal neuron activity was modulated by a variety of motor behaviors (straight run, right, left turn, straight + right turn, etc.). Such activity was correlated to the sequence of movements irrespective of the places where these movements occurred. A direction-dependent activity was found only in restricted portions of the paths suggesting a limited influence of the spatial context to parietal neuron activity. Thus, the finding suggests that parietal neurons encode representations of routes mainly in terms of movement sequences. Consistent with previous data, Nitz's results indicate that the parietal cortex not only is involved in the processing of motion information but also encodes representation of complex sensory motor behavior.

7. The role of the parietal cortex in the formation of spatial representation

Overall, lesion and electrophysiological studies provide a complex pattern of results that may reflect the multiple facets of parietal cortex functioning. It may also reflect neuroanatomical heterogeneity of this area. Note that little is known about the organization of inputs and outputs within the cortex parietal. It is likely that there is a subregional specificity. For example, a subregion may be preferentially involved in the processing of sensory information (e.g. visual) and another subregion in the association between tactile and visual information. Uncovering this organization may be very helpful to enhance our understanding of the multiple functional aspects of the parietal cortex.

The picture that emerges from the data ascribes to the parietal cortex a role in the processing of both allocentric and egocentric information. It is clear however that the parietal cortex does not play a role in all allocentric and egocentric processes but has a more specific function. The data first suggest that the parietal cortex is important when the animal has to form an allocentric spatial representation by using nearby cues. We have previously suggested that, in the nearby object situation, extraction of spatial invariants is strongly dependent on the association between different views of the environment and the movements connecting these views (Poucet, 1993; Poucet & Benhamou, 1997). Thus, one basic function of the parietal cortex would be to perform associations between visual information and motion information, a process that is an early and important step for the formation of a spatial representation (McNaughton, 1987). This hypothesis is consistent with neuroanatomical and functional data, accounting for

the diversity of behavioral lesion effects and firing correlates of parietal neurons reviewed above.

In a previous theoretical work (Save & Poucet, 2000b), we have proposed that the parietal cortex primarily processes spatial information in an egocentric frame of reference. Indeed, visual input from an animal's point of view as well as movement-related information are basically egocentric. Associations between views and motions are assumed to initiate the transformation of egocentric into allocentric information. Evidence for such a gradual process in the parietal cortex is provided, in particular, by unit recordings that have identified firing correlates ranging from pure motor to complex visuo-spatial-motor combinations (Chen et al., 1994a; McNaughton et al. 1989, 1994; Nitz, 2006). Accordingly, a number of deficits in allocentric tasks may be a consequence of upstream alteration in the transformation process. The egocentric-to-allocentric hypothesis still holds at the light of the most recent results even if it raises several questions. First, to what extent does the parietal cortex mediate the egocentric-to-allocentric conversion? Second, provided that the conversion is important for elaborating an allocentric representation, why should a parietal lesion not impair all behaviors requiring such a representation? Third, how is it possible to relate this particular function to other potential functions of the parietal cortex for example in attentional processes (e.g. Cabeza, Ciaramelli, Olson, & Moscovitch, 2008)? Fourth, is this role compatible with a possible implication in the long-term storage of allocentric spatial representations? Clearly, any global model of parietal functioning must answer these questions and integrate all these aspects.

8. The parietal cortex as an element of the cortical-hippocampal interaction

Understanding the role of the parietal cortex in spatial information processing requires taking into account its interactions with other cortical and subcortical regions. The data demonstrate that the parietal is functionally related to the hippocampus, thus supporting the idea that the parietal cortex is part of a functional network that allows continuous dialog between the neocortex and the hippocampus. The data also indicate that the parietal cortex and the hippocampus have distinct roles in spatial tasks. As proposed by Burgess, Jeffery, and O'Keefe (1999), there are two theoretical extreme views of the cooperation between the parietal cortex and the hippocampus. On the one hand, these two structures can be hypothesized to work in series. The parietal cortex would process sensory information in a format that could be used and further processed by the hippocampus. On the other hand, these two structures can be hypothesized to work in parallel. The parietal cortex and the hippocampus would mediate the formation of complementary spatial representations and parietal-hippocampal cooperation would then take place at all levels of processing. According to the serial hypothesis, a parietal cortex lesion may produce equivalent deficits as those resulting from hippocampal lesions, which is clearly not the case as shown by the short review of the literature presented above. According to the parallel hypothesis, a parietal lesion would be less disruptive than in the serial model, due to the spared capacity of the hippocampus to generate a spatial representation. This hypothesis accounts only partially for the behavioral effects of parietal cortex lesions. Thus, it could be useful to consider a model that comprises both serial and parallel properties. One possibility for integrating these two aspects would be to ascribe to the parietal cortex a role in both the processing of sensory information (serial processing in the egocentric-to-allocentric hypothesis) and in the long-term storage of spatial representations (parallel processing). This latter aspect is supported by metabolic imaging studies (Bontempi, Laurent-Demir, Destrade, &

Jaffard, 1999; Maviel et al., 2004) but needs to be further investigated.

The interest for the parietal cortex function in the spatial processing of information may have a new impetus as a consequence of the discovery of grid cells in the entorhinal cortex. These cells exhibit location-specific activity and generate multiple fields with regular spacing, therefore forming a grid-like firing pattern (Hafting, Fyhn, Molden, Moser, & Moser, 2005). It has been hypothesized that grid cells are involved in path integration, a basic navigation strategy requiring the use of movement-related information (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006 for a review). How grid cell activity is generated remains unknown so far. That the parietal cortex is involved in the processing of movement-related information and in path integration (Save et al., 2001) suggests that it could contribute to the generation of the grid cell signal. Other cortical areas projecting to the entorhinal cortex may also contribute to grid cell activity, in particular, the retrosplenial cortex. This region has been shown to be connected to both the parietal and entorhinal cortices and contains spatial, head direction and movement-related signals (Chen et al., 1994a; Cho & Sharp, 2001).

The parietal cortex occupies a unique position in the brain linking perception to spatial representations. Data have accumulated across years but the role of this region remains unclear. The difficulty is to integrate the different facets of its function into a coherent model. This model would necessarily have to also integrate the notion of a functional cooperation with the hippocampus and other cortical areas. Further anatomical, lesion and recordings studies are needed to enter into the details of the parietal contribution to spatial processing. In particular, the possibility of functional subdivisions may be investigated. Because there are similarities between rodents and primates, a functional model of the parietal cortex in the rat may be useful to understand the normal and pathological functioning of the human parietal cortex.

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