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

Etienne Save *, Bruno Poucet

Laboratory of Neurobiology and Cognition, UMR 6155, Aix-Marseille Université, CNRS, Pôle 3C, 3 Place Victor Hugo, 13331 Marseille Cedex 3, France

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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.

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 specific 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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* Corresponding author. Fax: +33 488 57 68 72.
E-mail address: etienne.save@univ-provence.fr (E. Save).

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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 connection are not specific since the lateroposterior nucleus also have 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 however 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 (Parron, Poucet, & Save, 2001). Using a distributed learning procedure, we found that short-lasting reversible inactivation of the dorsal

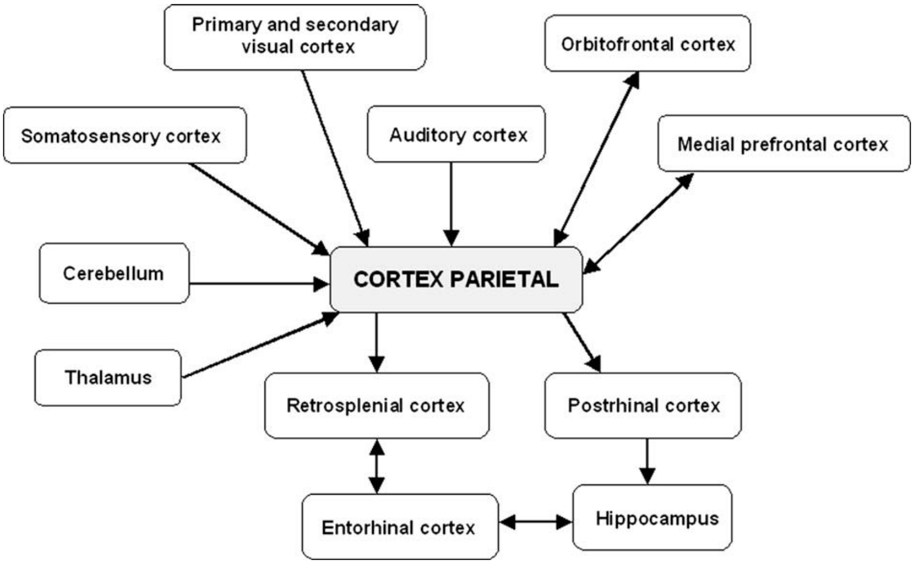

Fig. 1. Main cortical and subcortical connections of the parietal cortex in the rat.