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When is the perirhinal cortex necessary for the performance of spatial memory tasks?

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Abstract

The perirhinal cortex and hippocampus have close anatomical links and it has, therefore, been proposed that they have important, coordinated roles in memory. This review examines the relative role of these structures in spatial memory tasks that are known to be hippocampal-dependent. The published lesion data gives a mixed picture, as only some studies detect spatial deficits after perirhinal cortex lesions. The possible reasons for these inconsistencies are reviewed, along with electrophysiological data that indicate how perirhinal cortex lesions may alter neuronal activity in the hippocampus. Overall, the disruptive effects of perirhinal lesions on spatial memory performance are, when they occur, typically transient and never as severe as those seen after hippocampal lesions. It is argued that parallel cortical routes provide key, sensory data to the hippocampus such that in the absence of the perirhinal cortex alternative information is available. The deficits associated with perirhinal damage may then reflect difficulties that arise when task performance requires the use of ambiguous distal cues, for example, those containing overlapping visual features.

Keywords: Perirhinal cortex; Parahippocampal gyrus; Hippocampus; Spatial memory

The perirhinal cortex (areas 35 and 36), which forms part of the parahippocampal region, has direct anatomical connections with the hippocampus (Fig. 1). It also has dense, reciprocal connections with the entorhinal cortex which, in turn, is connected to the hippocampus (Fig. 1). Through these direct and indirect links the perirhinal cortex can influence the hippocampus [1,2]. Both the perirhinal cortex and the hippocampus are regarded as key regions for aspects of memory, and by virtue of their interconnections these mnemonic roles are often seen as being tightly linked. The extent to which these two regions are involved in the same classes of memory has, however, become a contentious topic (for contrasting views see [3–5]).

The purpose of this review is to consider the importance of the perirhinal cortex for one aspect of memory, spatial memory. To be more specific, this review will examine those aspects of spatial memory that are dependent on an intact hippocampus. In view of their connections, the discovery that the perirhinal cortex is also necessary for spatial memory would provide an important confirmatory step in the notion of an interdependent perirhinal–hippocampal memory system. Although research with nonhuman primates will be described, this review will focus primarily on data from studies with rats. This is because the large majority of relevant studies have been carried out with this species. It is, therefore, important to appreciate that a similar pattern of anatomical relationships exists between the perirhinal cortex and the hippocampus in both the rodent and the primate brain [6].

This review was prompted by the fact that a glance at the relevant lesion data will show that they are contradictory, and that by carefully picking the right references it is possible to support almost any viewpoint. Thus, for a range of different spatial tasks that are consistently sensitive to hippocampal damage (Morris water maze, radial-arm maze, T-maze alternation, delayed nonmatching-to-position), some studies have found normal performance following

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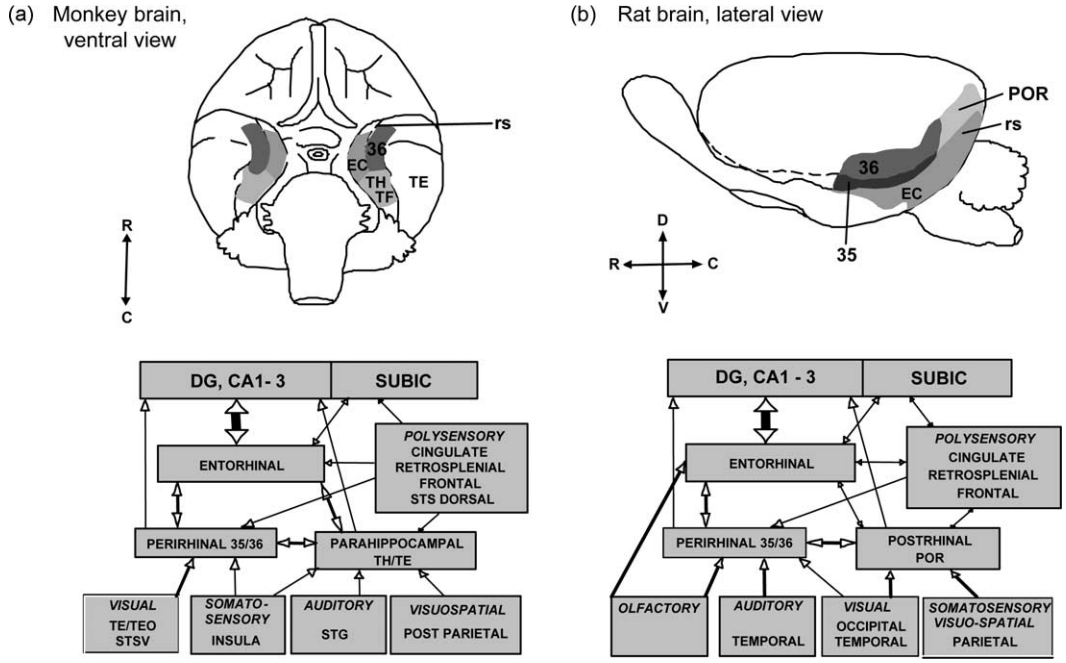

Fig. 1. Anatomical connections of the perirhinal cortex with the hippocampus and surrounding regions. The positions of the perirhinal, entorhinal, parahippocampal and postrhinal cortices are shown in the monkey (macaque) brain (a) and the rat brain (b). The perirhinal cortex, as defined here, includes Brodmann's areas 35 and 36 [6]. The term hippocampus refers to the dentate gyrus, subfields CA1-3 of the hippocampus and the subicular complex. The connectional diagrams show parallel routes by which sensory information reaches these cortical regions and from there reaches the hippocampus [6,111–115]. The thickness of the arrows indicates the size of the projection. (DG, dentate gyrus; EC, entorhinal cortex; POR, postrhinal cortex; rs, rhinal sulcus; STG, superior temporal gyrus; STSV, superior temporal sulcus ventral; SUBIC, subicular complex). Adapted with permission from Burwell et al. [6].

perirhinal lesions while an almost equal number have found impairments. Some studies have even found evidence for enhanced performance after perirhinal lesions. The uncertainty generated by these conflicting results is delaying progress in creating more formal models of the functional relationships between the perirhinal cortex, the hippocampus, and the remainder of the parahippocampal region [7,8].

Our strategy will be to consider first those general methodological features that might account for these differences in the effects of perirhinal lesions. This is followed by a detailed consideration of the findings for different types of spatial tasks. These tasks will be dealt with separately as they make varying demands on the animals. Unless it is specifically stated, the information refers to studies on the rat brain. The outcome of this initial review will then be placed in the context of other forms of evidence, in particular, single cell recording studies in normal rats and in rats with perirhinal lesions.

1. Lesion evidence

As outlined above, the effects of perirhinal lesions on tests of spatial memory are remarkable for their degree of inconsistency. Just as a large number of papers have reported no lesion induced deficits [9–18], so have an equally large number found impairments [19–29].

1.1. Extent of perirhinal damage

The perirhinal cortex lies in the rhinal sulcus and extends rostro-caudally for a distance of approximately 4.5 mm in the rat brain. In view of its shape and historical variation in the definition of its borders [1,6] it is not surprising that the extent of perirhinal surgeries has sometimes varied. This leads to perhaps the most obvious explanation for the inconsistent findings in the literature: those studies associated with lesion-induced deficits have a more complete removal of the perirhinal cortex. In fact, an examination of the published data rapidly shows that this is not the case.

The most complete perirhinal lesions are almost certainly those in which the surgery was deliberately extended caudally to include the postrhinal cortex [11,13,14]. This ensures that there is no sparing of the caudal perirhinal cortex. At the same time, these same lesions extended rostrally to incorporate almost all of the anterior perirhinal cortex. In spite of the completeness of the lesions and the use of a range of spatial tasks (Morris water maze, T-maze, radial-arm maze), none of these studies [11,13,14] reported a lesion-induced deficit.

An inspection of the extent of those lesions that were targeted at just the perirhinal cortex also fails to support the premise that lesion size is the key factor. Some of the most discrete lesions appear to be those by Wiig and Bilkey [19,28] where there is some sparing of the rostral perirhinal cortex. Nevertheless, in both studies the lesions produce