



Short communication

The retrosplenial cortex is necessary for path integration in the dark



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HIGHLIGHTS

- Rats with retrosplenial cortex lesions were trained in a path integration task with minimal memory requirements, in light and darkness.
- Lesioned and sham groups used a path integration strategy in both lighting conditions.
- Lesioned rats showed path integration impairment in darkness but not in light.
- The retrosplenial cortex is important for path integration and incorporates visuospatial information, irrespective of task-related spatial memory, to maintain path integration accuracy.

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ABSTRACT

An increasing amount of data indicates that the retrosplenial cortex (RSC) plays a role in navigation and spatial memory. Moreover, it has been suggested that the RSC integrates mnemonic spatial features of the environment with self-motion information therefore enabling accurate path integration in darkness. This hypothesis rests on data obtained from animals trained in spatial memory tasks involving the conjoint use of allothetic and idiothetic information [8]. We examined the contribution of the RSC when animals are submitted to a path integration task with minimal memory requirement in light and dark. We found that RSC-lesioned rats exhibited a path integration deficit in the dark but not in the light. This suggests that the RSC is important for path integration and incorporates visuospatial information to maintain path integration accuracy.

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Navigation in animals depends on both self-motion (idiothetic) and external (allothetic) information. When allothetic information is absent or irrelevant, idiothetic cues (i.e. vestibular, somatosensory, proprioceptive information, optic flow) enable navigation by path integration [1]. The animal is then able to return straight to a starting location (e.g. a nest) from any point of its searching path. In recent years there has been a growing interest in the neural bases of path integration. Lesion and electrophysiological studies have suggested that path integration is mediated by a network of brain structures which are part of the cortical–hippocampus axis. Thus, most theoretical accounts assume that idiothetic information is processed and conveyed to the hippocampus via a number of cortical areas such as the parietal, the entorhinal and the retrosplenial cortices (RSC) [1]. The RSC is divided into a dysgranular (area 30) and granular (area 29) regions [2,3] and has connections with a number of sub-cortical and cortical regions. In particular

it has reciprocal connections with the visual areas [4] and is connected with regions that have been suggested to play a role in the processing of idiothetic information such as the parietal cortex and the entorhinal cortex [3–6]. This pattern of connectivity suggests a contribution to the processing of multimodal information.

Consistent with the connectivity, it has been shown that the RSC is important for navigation in total darkness suggesting a role in path integration [7]. Another hypothesis was proposed by Cooper et al. based on the effect of RSC inactivations in reference and working spatial memory tasks in light and darkness. They proposed that the RSC is involved in association between landmark-based spatial memory and self-motion information [8]. It is possible however that this putative function resulted from the memory requirements of the task therefore masking path integration impairment. To clarify the involvement of the RSC in path integration and its role in associating visuospatial and idiothetic cues, we investigated the effect of RSC lesions in a path integration task with minimal memory requirements, in light and dark conditions.

Fifteen Long Evans 300 g male rats (Janvier, St Berthevin, France) were trained in a hoarding task, adapted from the Whishaw Foraging Task [9], on a white circular elevated platform (190 cm diameter, 85 cm above the floor) located in a well-lit room [10,11].

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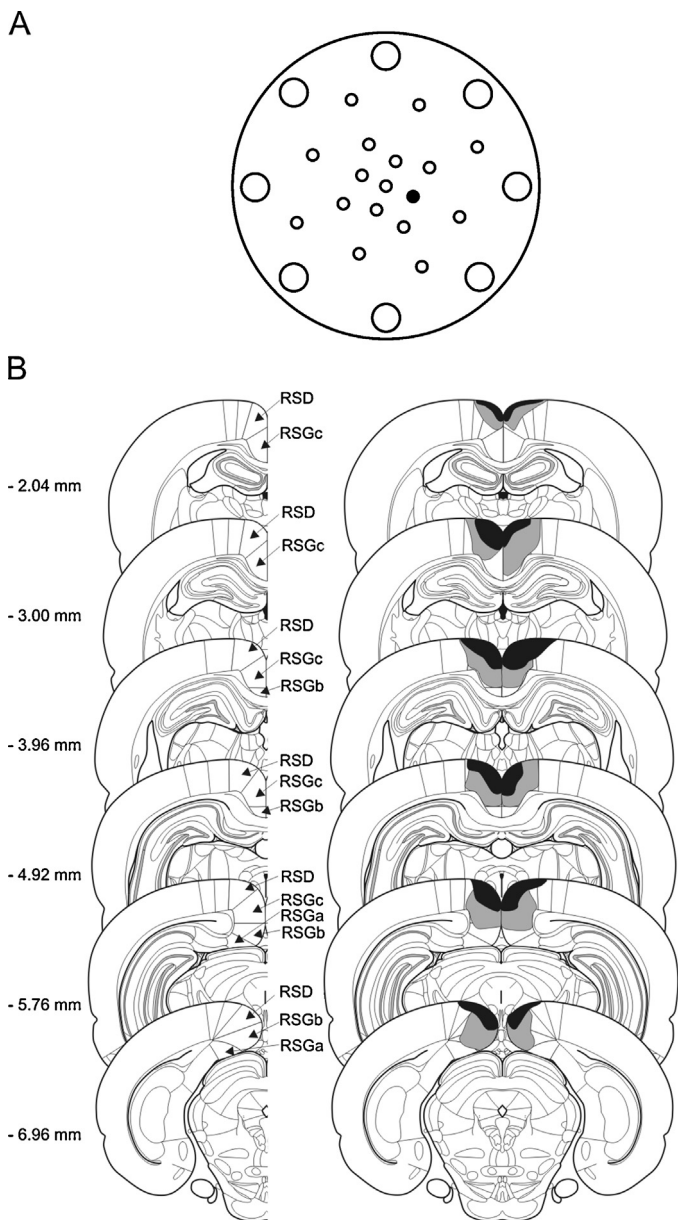


Fig. 1. (A) View from above of the apparatus. See text for details. The eight peripheral circles are the possible starting places. The small circles are the 17 cups that could contain a piece of food. In each trial only one cup among the 17 (in black) is rewarded. (B) Histology. Right panel: coronal sections at six levels relative to bregma (in mm) showing maximal (black) and minimal (dark gray) extent of the lesions. Large lesions have been found in 3 rats and small lesions in 6 rats. The different areas of the retrosplenial cortex are indicated on the left panel, RSD retrosplenial dysgranular cortex, RSGa,b,c retrosplenial granular cortex (adapted from [12]).

Eight peripheral holes (12 cm diameter) served as starting places for the animals. Seventeen gray polyvinyl chloride cups that could contain a piece of food pellet were distributed all over the platform (Fig. 1A). The animal was brought from the colony room in a transportation box containing sawdust which was placed under one of the eight peripheral holes. Environmental cues were carefully controlled to prevent animals to use an allothetic cue-based strategy. The apparatus was surrounded by a white opaque circular curtain to eliminate remote visual cues. The experimenter was located outside the curtain enclosure at all times, remaining still and silent as soon as the transportation box was placed under the starting hole and until the end of the trial. A radio set fixed to the ceiling in a central position produced background noise >70 dB to mask auditory

directional cues. To neutralize directional olfactory cues, 7 boxes similar to the transportation box, also containing soiled sawdust, were placed under each of the remaining peripheral holes. In addition, the platform was entirely cleaned with 90° alcohol between each trial. More generally, to prevent the animal from relying on remote cues in the room reference frame, the starting hole and baited cup were different on each trial. After their body weight was reduced to 85% of the initial weight as a result of a progressive food deprivation schedule, the animals were submitted to a training phase and a test phase. The animals were progressively trained so that at the end of training, they readily jumped through the hole on the platform, explored it until they find the baited cup, took the pellet and carried it back directly to a hole. If the return hole was the starting hole they could enter it and eat the food pellet. If it was not the starting hole they were allowed to reach other holes until they find the correct one. Training included 2 phases. In the first phase all 17 cups were baited. Rats were submitted to 2 trials a day during which they could leave and return to the home box, as many times as they wanted until they carried back one pellet or until 20 min have elapsed. As soon as they had carried back a pellet in the home box the trial was stopped and animals were allowed to eat quietly for a few minutes. This phase was completed when they returned to the home box with a pellet in 3 consecutive trials. In the second phase only one cup was baited. This phase was completed when the animals performed the expected behavior and returned to the home box in only one trip and less than 2 min in 3 consecutive trials.

Following training, a group (RETRO, $n=9$) received a bilateral thermocoagulation lesion of the RSC (anesthesia, xylazine 15 mg/kg and ketamine 100 mg/kg, i.p.). A bone window was removed at the coordinates AP -2.8 mm $L \pm 0.5$ mm, AP -3.8 mm $L \pm 1.2$ mm, AP -4.3 mm $L \pm 1.7$ mm, AP -6.7 mm $L \pm 1.2$ mm, AP -7.6 mm $L \pm 1.4$ mm [12] and the exposed brain was damaged by briefly and touching the dura at various points with a calibrated heating resistance (120°C). The skin was sutured and the animal was placed in a recovery room (22°C) for 3 days before being returned to the colony room. Pre- and post-surgery treatment included a long action antibiotic (amoxicilline, 0.05 ml, s.c.) and an analgesic (tolfedine, 0.03 ml, s.c.). Sham-lesioned rats (SHAM, $n=6$) were submitted to the same surgery procedure except that no thermocoagulation was applied. The procedure was approved by the local ethic committee, authorization #A81212 and the experiments were performed in accordance with European (European Community Council Directive 86/609/EEC) and national guidelines (Council Directive 87848 and permission #13.24 to ES). Ten days after surgery, rats were briefly re-trained and were submitted to 34 test trials (2 trials a day to avoid intra-day satiety effects) with a different starting hole and baited cup on each trial. Thus, all rats experienced all ranges of distance between the starting hole and the baited cup. A thin wire mesh, only visible from above the hole, was placed on the incorrect holes to prevent rats from entering these holes. In a typical test trial, in light or dark, the home box containing the rat was placed under one of the 8 holes. The rat then jumped onto the platform and visited the cups until it found the pellet, took it in its mouth and returned in a relatively straight path to the hole leading to the home box (correct response) or to another hole (incorrect response). In case of an incorrect response, the rat was allowed to visit other holes until it reached the correct one. Once in the home box the rat was let to eat the pellet and was then returned to its home cage located in a different room. Following the first test phase, the rats were submitted to a second test phase to examine path integration performance in darkness. Rats received 17 trials using the same protocol as in the light test phase except that all manipulations were made in total darkness. The animal's position was monitored by a tracking system (Videotrack, Viewpoint, France) in both light and darkness. In darkness, a small battery-powered infrared

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