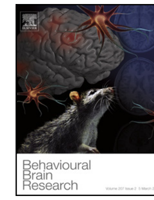
Behavioural Brain Research 292 (2015) 1–9

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr




Research report

# The role of rat posterior parietal cortex in coordinating spatial representations during place avoidance in dissociated reference frames on a continuously rotating arena (Carousel)

Jan Svoboda[a,*], Petr Telensky[a,b,c], Karel Blahna[a], Martin Vodicka[a], Ales Stuchlik[a,d]

[a] Institute of Physiology of the Czech Academy of Sciences, Prague, Czech Republic
[b] Department of Physiology, Faculty of Science, Charles University, Prague, Czech Republic
[c] International Clinical Research Center, St. Anne's University Hospital Brno, Brno, Czech Republic
[d] National Institute of Mental Health, Klecany, Czech Republic

## HIGHLIGHTS

- Posterior parietal cortex (PPC) lesioned rats were tested in Carousel maze.
- PPC rats were impaired in flexible use of extramaze cues.
- PPC rats were impaired in proximal, but not distal, cues navigation in water maze.
- PPC lesion impairs flexible use of behavioral strategies under high cognitive load.

## ARTICLE INFO

*Article history:*
Received 6 January 2015
Received in revised form 5 May 2015
Accepted 8 May 2015
Available online 16 May 2015

*Keywords:*
Posterior parietal cortex
Reference frame
Navigation
Lesion
Rat

## ABSTRACT

On the Carousel maze, rats are trained to avoid a sector of a circular rotating arena, punishable by a mild electric foot-shock. In the room frame (RF) variant, the punishable sector remains stable relative to the room, while in the arena frame (AF) version, the sector rotates with the arena. The rats therefore need to disregard local olfactory, tactile and self-motion cues in RF condition and distal extra-maze landmarks in the AF task. In both primates and rodents, the coordination of various spatial reference frames is thought to depend on the posterior parietal cortex (PPC). We have previously shown that PPC-lesioned rats can solve both variants of the Carousel avoidance task. Here we aimed to determine the effects of bilateral thermocoagulation lesion of the PPC in Long–Evans rats on the ability to transition between multiple spatial strategies. The rats were first trained in five sessions in one condition and then another five sessions in the other. The following training schemes were used: RF to AF, RF to RF reversal (sector on the opposite side), and AF to RF. We found a PPC lesion-associated impairment in the transition from the AF to RF task, but not vice versa. Furthermore, PPC lesion impaired performance in RF reversal. In accordance to the literature, we also found an impairment in navigation guided by intra-maze visuospatial cues, but not by extra-maze cues in the water maze. Therefore, the PPC lesion-induced impairment is neither specific to distant cues nor to allocentric processing. Our results thus indicate a role of the PPC in the flexibility in spatial behaviors guided by visual orientation cues.



## 1. Introduction

Locations in an environment can be encoded with respect to different frames of reference. Usually, we consider two principal referencing systems: egocentric (body-centered), further specified as retino-, head-, or trunk-centric; and allocentric (body independent) which can be arbitrarily centered on any point within the environment. Behavioral activities, such as spatial navigation, reaching and grasping require translation of information coded in distinct spatial frames into purposeful thinking and behavior. In primates, it is believed that the principal brain structure providing these computations is the posterior parietal cortex – PPC [1].

Rodent associative cortex located between occipital and somatosensory cortices considered an analog of the primate PPC

* Corresponding author at: Institute of Physiology of the Czech Academy of Sciences, Videnska 1083, 14220 Prague 4, Czech Republic. Tel.: +420 24106 2713; fax: +420 24106 2488.
*E-mail address:* svobodaj@biomed.cas.cz (J. Svoboda).

http://dx.doi.org/10.1016/j.bbr.2015.05.008

**Table 1**
Group averages (±S.E.M.) of maximum inter-entrance interval (MaxT) and the latency to the first entrance (Lat1E) for the first and last session in a particular phase of a given experiment.

| | MaxT (s) | | Lat1E (s) | |
|---|---|---|---|---|
| | Sham-operated | Lesioned | Sham-operated | Lesioned |
| **Exp. 1** | | | | |
| RF avoidance (session 1–5) | 382.5 ± 52.2–654.3 ± 61.6 | 300.4 ± 78.0–587.5 ± 83.5 | 37.9 ± 11.5–293.9 ± 105.6 | 4.86 ± 2.02–109.1 ± 30.7 |
| AF avoidance (session 6–10) | 235 ± 49.9–531.2 ± 54.5 | 425.7 ± 100.3–548.7 ± 59.4 | 44.9 ± 9.1–162.6 ± 59.3 | 150.5 ± 120.4–159.9 ± 82.7 |
| **Exp. 2** | | | | |
| RF avoidance (session 1–5) | 362.9 ± 64.7–952.1 ± 67.3 | 229.6 ± 41.1–617.0 ± 101.4* | 13.7 ± 6.6–625.5 ± 158.7 | 18.2 ± 11.1–414.4 ± 129.1 |
| RF reversal (session 6–10) | 504.0 ± 73.9–767.0 ± 113.6 | 226.4 ± 57.2–661.4 ± 124.6* | 5.0 ± 1.8–299.3 ± 160.5 | 8.3 ± 4.7–269.9 ± 148.9 |
| **Exp. 3** | | | | |
| AF avoidance (session 1–5) | 495.7 ± 78.2–618.6 ± 58.3 | 495.7 ± 78.2–618.6 ± 58.3 | 16.5 ± 4.9–312.1 ± 68.2 | 11.6 ± 5.6–625.0 ± 192.0 |
| RF avoidance (session 6–10) | 307.6 ± 69.3–589.1 ± 64.2 | 183.4 ± 21.3–419.3 ± 46.5* | 32.3 ± 6.7–32.0 ± 12.8 | 45.0 ± 13.2–55.9 ± 19.7 |

* Significant ($p < 0.05$) group effect.

[2,3] covers a substantially smaller surface of the telencephalon. It has been shown to play an important role in spatial representations, which is, however, not yet fully understood [2,4–7].

The first attempts to explain parietal function in terms of allocentric processing [8,9] need to be revised since both ablation experiments and electrophysiological recordings showed that the PPC is involved in both egocentric [10–12] and allocentric processing [2,13–15]. Moreover, lesions of the PPC do not prevent the use of egocentric [16] or allocentric information [15] per se. Current theories of rodent PPC function focus on integration of different reference frames into goal-directed behavior [7,12,14]. One of the explanations is based on a hypothesis that the PPC encodes information in both frames and deficits manifest as the load for the translator increases [6,15].

Active place avoidance on a Carousel requires the rats to avoid an unmarked place on a continuously rotating (1 rpm) circular arena [17–19] and allows assessment of the ability to segregate and coordinate spatial information bound to a particular reference frame. The rotation dissociates spatial cues in the environment into two independent reference frames of the rotating arena and stationary room. The to-be-avoided place can be defined in either the arena- or room-frame. Thus, in principle, we can use two variants of this task: a room-based task in light with emphasis on visual cues and arena-based task in darkness where navigation is guided by, largely self-generated, local cues on the arena floor. Notably, both tasks require segregation of stimuli room- and arena-cues into coherent subsets [20].

Our previous work found no effect of PPC lesions on navigation in either the arena- or room-frame [21]. However, the ability to select the relevant frame for navigation and switch to the other frame was not systematically analyzed in that study. Rodent PPC has been implicated in attention processes [22] and cognitive flexibility, particularly in extra-dimensional shift [23]. Our pilot data suggested that PPC lesions might affect the way rats use a relevant frame in the presence of cues from both frames. Therefore, we aimed to determine how PPC lesions affect segregation and flexibility in the use of the frame relevant for navigation. We hypothesized that PPC is involved in flexible switching from one frame of reference to the other and that deficit induced by PPC lesions will be most prominent during the first session after the switch and independent of its direction, i.e. from arena to room frame avoidance or vice versa (Table 1).

## 2. Materials and methods

### 2.1. Animals

Forty-eight male adult Long–Evans rats from the breeding colony of the Institute of Physiology were used in the study. They were three months old upon arrival and weighed 250–320 g. They were housed in groups of two or three per cage in a temperature-controlled animal room (21 °C) with a 12/12 h light/dark cycle (lights on at 7:00). Food and water were freely available until three days prior to behavioral training when the rats were food-restricted to maintain their weight at 90% of their free-feeding weight. All the experimental procedures were carried out during the light period of the day with the emphasis to test each animal in the same time period. The testing order of the animals was kept constant throughout the training and remained counterbalanced across groups. All the manipulations complied with the Czech Animal Protection Act, directive of the European Community Council (2010/63/EC), and NIH guidelines.

### 2.2. Surgery

Rats were randomly assigned to sham-operated (controls, $n = 24$) or posterior parietal cortex lesion (parietal, $n = 24$) groups. They were anesthetized with ketamine (50 mg/kg, i.p.) and xylazine (40 mg/kg, i.p.) and gently fixed in a stereotaxic frame (TSE systems). The head was shaved and the scalp was incised and retracted. The skull was cleared and two trephine openings were drilled into the skull to expose the brain at the following coordinates relative to the *bregma*: AP −2 to −6 mm, ML ±1.5 to ±5.5 mm. Bilateral thermocoagulation lesions of PPC were induced by applying the tip (diameter = 0.5 mm) of a calibrated soldering iron (temperature 180 °C) directly to the *dura mater* for 0.5 s at various points within the exposed area until the entire surface was lesioned. Sham-operated rats underwent the same procedure except for applying the soldering tip to the *dura*. Thermocoagulation lesions have been shown to be effective and safe for the animals [15,21]. Sterile gelfoam was then placed in the openings and the wound was sutured, followed by a local application of lidocaine and antiseptic. The rats were left to recover for at least 14 days. One sham-operated animal died during recovery period. A day before the start of the behavioral pretraining, awake animals were gently implanted with a hypodermic needle connector, which pierced the skin between rat's shoulders. The tip was blunted and swirled to prevent slipping out and to provide a purchase for an alligator clip connecting a shock-delivering wire.

### 2.3. Behavioral apparatuses

#### 2.3.1. Carousel

The Carousel [17,19,21,24] consists of a smooth metallic circular arena (82 cm in diameter) enclosed by a 30 cm high transparent Plexiglas wall. The arena is elevated 1 m above the floor of a 2 m × 3 m dimly illuminated room containing an abundance of extra-maze cues. An infrared light-emitting diode (LED) located