ELSEVIER

Behavioural Brain Research 104 (1999) 197–200

BEHAVIOURAL BRAIN RESEARCH

www.elsevier.com/locate/bbr

Short communication

Disorientation combined with bilateral parietal cortex lesions causes path integration deficits in the water maze

Sean Commins, Colin Gemmell, Michael Anderson, John Gigg, Shane M. O'Mara *

Department of Psychology, Aras an Phiarsaigh, University of Dublin, Trinity College, Dublin 2, Ireland

Received 9 July 1998; received in revised form 14 June 1999; accepted 15 June 1999

Abstract

The navigational abilities of rats were examined using the water maze after disorientation induced by rotation and/or swimming in darkness. Control and light-disoriented groups performed similarly, whereas the dark group and the dark-disoriented groups were initially much slower but improved to control levels. After receiving bilateral parietal lesions, multiple start position tests showed that both rotation groups were severely impaired in finding the hidden platform. The effects of disorientation induced by darkness and by rotation are therefore separable.

Keywords: Water maze; Path integration; Parietal cortex; Disorientation

1. Introduction

It is known that performance in the water maze is extremely sensitive to hippocampal lesions [6]. The hippocampal-based navigational system is thought to be an environment-centred (allocentric) spatial representation in which environmental events, cues or places are represented in relation to each other, rather than the animal itself. However, the brain also uses non-allocentric, internally-generated cues for spatial representation and navigation (see Ref. [11] for review).

'Path integration' is the determination of current position using self-motion cues [3]. This information can be used to estimate current position relative to an origin or an estimate of a trajectory towards a target. Many studies suggest that parietal cortex is one brain area where this egocentrically-based information converges [3,9]. It has been suggested that the parietal cortex acts as an interface for this egocentric coding and for allocentric information processed by the hippocampus [9]. Moghaddem and Bures [5] found that rats learned the platform position in darkness in the water maze, relying presumably on internally-generated cues to compute their position, although they learned more slowly than controls. Subsequently, Save and Moghaddem [8] found parietal cortex-lesioned rats had impaired water maze acquisition relative to controls in darkness, although retention was less impaired.

We further examine here the effects of disorientation by rotation/translation and/or darkness on water maze acquisition and subsequently of parietal cortex lesions combined with disorientation on reacquisition of the water maze.

2. Materials and methods

Twenty-three male Wistar rats (mean weight 200 g) were used. Rats were housed in groups of three on a 12:12-light/dark cycle with free access to food and water. The water maze was a black circular pool (2 m/diameter; 35 cm/deep; water 20 ± 1°C) filled to 31 cm. Rats could escape by climbing onto a hidden platform (29 cm × 9 cm). The maze was surrounded by retractable black curtains and had an overhead videotracking camera. The rats wore a table tennis ball

* Corresponding author. Tel.: +353-1-6081175; fax: +353-1-6712006.

E-mail address: smomara@tcd.ie (S.M. O'Mara)

0166-4328/99/$ - see front matter
PII: S0166-4328(99)00094-7

containing a small LED visible to the camera. The computer and video monitor were in one corner of the experimental room.

The rats received eight trials/day for each phase of the experiment, with a 1-min inter-trial interval and a 2-min trial limit, after which the rat was led to the platform. Group one (normal controls; $n = 6$) was trained under standard water maze protocol conditions; Group two (light-rotation; $n = 5$) was disoriented by taking the rats to the experimental room from their cages in an opaque covered box along a pathway involving multiple lateral displacements and complete rotations. The disorientation procedure was continued in the experimental room, prior to the rats being placed in the water maze. This group had a clear view of the experimental room. Group three (dark; $n = 6$) was trained in complete darkness, with the curtains around the maze closed. The behaviour of the animals was monitored on the video screen located outside the enclosed maze area. Group four (dark-rotation; $n = 6$) was disoriented in an identical fashion to the light-rotation group and also trained in the dark. The phases of the experiment were as follows:

1. Normal training: All rats were trained from a constant start position to a constant platform position (7 days, eight trials per day).
2. Variable start-position: The rats were placed in the pool from four start positions (N, S, E, W) for a further 3 days. After this phase all rats in all four groups underwent bilateral parietal cortex lesions (see below).
3. Post-surgery retraining: All rats were retrained for 5 days under normal conditions, as described above.
4. Variable start-position: All rats had 3 more days of variable-start position training (see (ii) above).

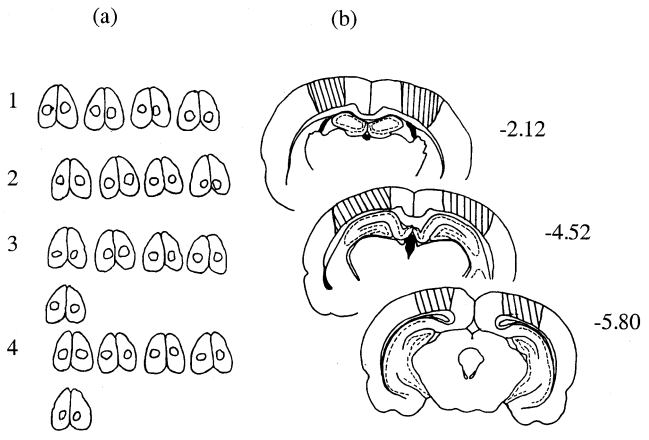

Fig. 1. (a): Parietal lesions, dorsal aspect. The numbers to left indicate to which group each of the rats belonged, as follows: group 1: controls; group 2: light-rotation; group 3: dark swimming; group 4: dark-rotation. (b) Maximal and minimal extent of the parietal lesions; the hatched areas indicate the extent of tissue at three different levels relative to bregma.

Each rat received a total of 144 trials over the four phases (18 days) of training; four animals did not complete all phases of the experiment and their data were discarded.

3. Results and discussion

For the surgery, rats were anaesthetised with pentobarbitone (50 mg/kg). Bilateral trephine openings were made A/P 2–6 mm and L 1.5–5.5 [4,7] and the underlying cortex was gently aspirated. Rats were allowed to recover for a minimum of 5 days before testing recommenced. At the end of the experiment, all rats were anaesthetised, transcardially perfused with saline followed by 4% formolsaline; the brains were removed and photographed prior to further histological processing. The largest and smallest lesions are presented in Fig. 1 (a, b).

The following results were found for each phase:

Phase one: Although all rats acquired the task prior to lesioning, there were significant differences between the groups. Fig. 2 (a) demonstrates that the escape latencies decreased across trials; (paired t-tests for all conditions day 1 × day 7, all cases $P < 0.001$). It can also be seen from Fig. 2 (a) that the rats in the dark conditions (groups three and four) were slower to learn than those in the light conditions; a one-way ANOVA (condition × latency) found a significant overall difference between groups, $F(3, 1066) = 7.01$, $P < 0.001$). *Post hoc* testing (Newman–Keuls) revealed that groups three and four were significantly different from groups one (controls) and two (light-rotation) ($P < 0.05$). We also conducted a series of ANOVAs comparing performance within days. Inspection of Fig. 2 (a) demonstrates that on days 1 and 2 all groups started with approximately the same level of performance (both ANOVAs were NS). However, the groups were significantly different from each other on days 3 through 7 (all ANOVAs $P <$ 0.001; df 3, 180).

Phase two: All rats across all conditions showed equally good performance when tested from variable starting positions. There were no significant differences between any of the groups for any of the possible comparisons. Inspection of trial blocks 8, 9 and 10 shows that all animals have similar escape times.

Phase three: Parietal lesions were conducted prior to this phase of the experiment. All animals in all groups were significantly impaired in their initial performance after lesion compared to their terminal performance prior to lesions; (paired t-tests for all conditions day 10 × day 11, all cases $P < 0.001$). Fig. 2 (b) indicates that escape latencies decreased across trials for all groups in this phase of the experiment

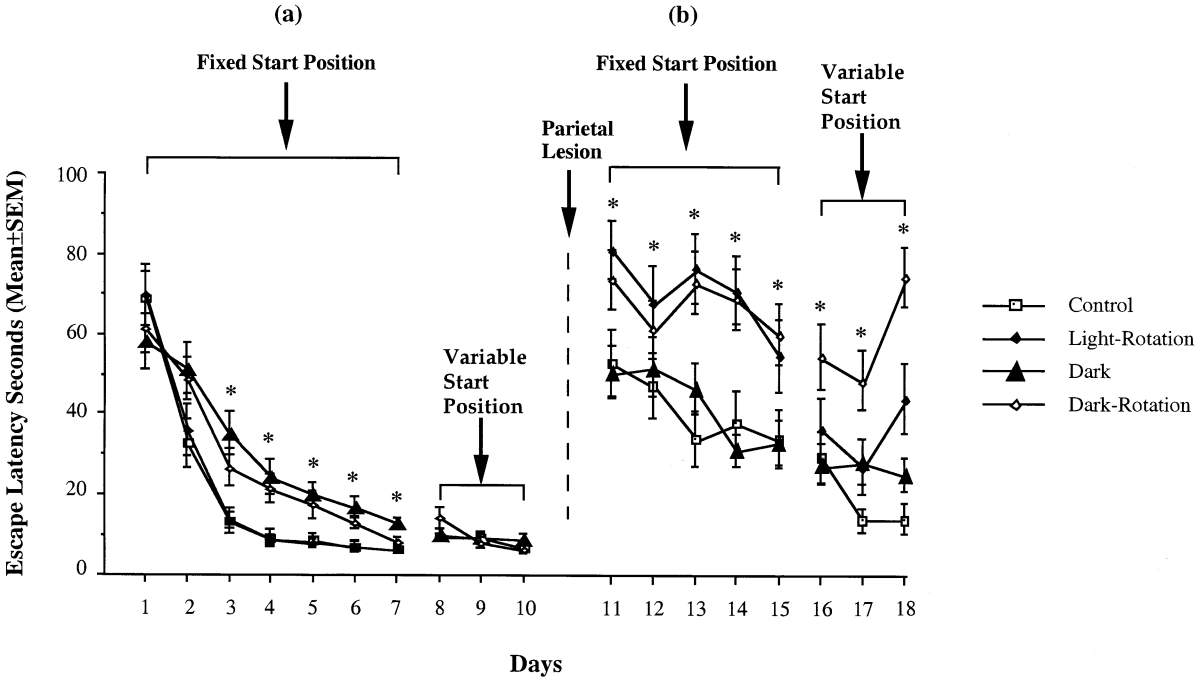

Fig. 2. (a): Effects of training from a standard start position on finding the hidden platform from differing start positions. On days 3 through 7, the asterisks refer to significant within-day differences between groups at $P < 0.001$. (b) Effects of training from a standard start position on finding the hidden platform from different start positions after parietal lesions. On all days, the asterisks refer to significant within-day differences between groups with probability values ranging from < 0.03 to < 0.001 for different days and which are specified in the result sections for phases 3 and 4.

(paired t-tests for all conditions: day 11 × day 15, all cases $P < 0.001$). There was also a significant difference between groups for all days from day 11 through day 15 (all ANOVAs $P < 0.001$; df 3, 140, except day 15, $P < 0.01$). *Post hoc* tests indicated that across days 11–15 groups one and three were significantly different to groups two and four ($P < 0.05$), indicating that groups one and two were significantly faster in re-acquiring the task post-lesion, compared to groups two and four. In contrast to phase one of the experiment, the performance of group two was the slowest between days 11 and 14, and was slower than groups one and three on day 15. The performance of this group mirrored that of group four (dark-rotation). The groups subjected to rotation were the most significantly impaired across all days of this phase of the experiment.

Phase four: In contrast to phase two, there were large differences in the performance of all groups in the final phase of the experiment through all experimental blocks (all ANOVAs $P < 0.001$; df 3, 140, except day 16, $P < 0.01$). *Post hoc* tests indicated that across phase four of the experiment group four (dark-rotation group) was significantly slower at finding the platform from a variable start position compared with all other groups; group two (light-rotation group) was also significantly slower than the other groups on day 18. At the end of the experiment, the escape latency (mean ± SEM) for groups two and four were 41.1 ± 8.5 s and 74.6 ± 7.7 s, respectively.

This experiment examined the effects of disorientation (through visual deprivation and/or rotations/translations) and parietal cortex lesions on path integration in the water maze. There were three main findings: (i) disoriented animals (whether induced by darkness and/or rotations and translations) are capable of finding a hidden platform in the absence of external cues, although at a slower rate than under normal illuminated conditions; (ii) the parietal lesions used in this experiment greatly disrupted the reacquisition of the original task and effectively abolished reacquisition in the dark rotation group; and (iii) the additive effect of rotation to swimming in the light or the dark greatly disrupts performance after bilateral lesions compared to swimming in the dark or light with a lesion alone.

Possibly the simplest interpretation of the first finding is that the period of disorientation forced the animals to rely entirely on self-generated motion cues and to ignore any possible maladaptive visual cues that may have been present. Animals without a parietal cortex subjected to vestibular stimulation show deficits in performance relative to those who have not; this situation is mirrored in studies with humans with right parietal lesions [1,2].

These finding extend those of Moghaddem and Bures [5], and Save and Moghaddem [8]. The fact that ani-

mals in the present experiment were capable of finding the platform rapidly and easily from a variety of different start positions prelesion, despite training from just a single start position suggests that, under normal conditions, egocentrically-based experience may map onto an allocentric representation under a range of conditions. The animals were not trained to find the platform from multiple start positions and did not experience multiple trained trajectories from differing positions at the boundary of the maze. This rules out simple route learning strategies for finding the platform. A greater reliance on auditory cues during training for both dark groups compared to the two light groups cannot be ruled out.

The present results provide further evidence that the effects of disorientation induced by darkness and by rotation can be separated. In addition, they support the idea that the rodent parietal cortex, in a manner similar to that of the primate, may act as an interface for both allocentric and egocentric information [9,10].

Acknowledgements

This research was supported by the Wellcome Trust, the European Commission, Enterprise Ireland, and the Arts and Social Sciences Benefaction Fund of Trinity College. We thank Ian Robertson, Department of Psychology, Trinity College, Dublin, Ireland, and Vincent Walsh, Department of Experimental Psychology, University of Oxford, Oxford, UK for helpful discussions regarding this paper.

References

[1] Farrell MJ, Robertson IH. The automatic updating of egocentric spatial relationships and its impairment due to right posterior cortical lesions. Neuropsychologia 1999;in press.
[2] Farrell MJ, Robertson IH. Mental rotation and the automatic updating of body-centered spatial relationships. J Expt Psychol Learning Memory Cognition 1998;24:227–33.
[3] Glasauer S, Amorium MA, Vitte E, Berthoz A. Goal-directed linear locomotion in normal and labyrinthine-defective subjects. Expt Brain Res 1994;98:323–35.
[4] Kolb B, Walkey J. Behavioral and anatomical studies of the posterior parietal cortex in the rat. Behav Brain Res 1987;23:127–45.
[5] Moghaddem M, Bures J. Contribution of egocentric spatial memory to place navigation of rats in the Morris water maze. Behav Brain Res 1996;78:121–9.
[6] Morris RGM, Garrud P, Rawlins JNP, O'Keefe J. Place navigation impaired in rats with hippocampal lesions. Nature 1982;297:681–3.
[7] Paxinos G, Watson C. The Rat Brain in Stereotaxic Coordinates, 2nd edition. San Diego, CA: Academic Press, 1986.
[8] Save E, Moghaddem M. Effects of lesions of the associative parietal cortex on the acquisition and use of spatial memory in egocentric and allocentric navigation tasks in the rat. Behav Neurosci 1996;110:74–85.
[9] Save E, Poucet B, Foreman N, Thinus-Blanc C. The contribution of the associative parietal cortex and hippocampus to spatial processing in rodents. Psychobiology 1998;26(2):153–61.
[10] Stein JF. Space and the parietal association areas. In: Paillard J, editor. Brain and Space. Oxford: Oxford University Press, 1991.
[11] Wiener SI, Berthoz A. Vestibular contributions during navigation. In: Berthoz A, editor. Multisensory Control of Movement. Oxford: Oxford University Press, 1993.