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Short communication

Changes to open field surfaces typically used to elicit hippocampal remapping elicit graded exploratory responses

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A B S T R A C T

Studies show that changes in environmental context alter the spatial firing patterns ('remapping') and increase immediate early gene activation in hippocampal but not subicular neurons. However, such studies rarely report co-occurring behavioural responses. We examined the behavioural effects of habituating rats to a walled open field, and then of changing the environmental context by altering wall patterns and floor colour. These kinds of cue change are known to elicit spatial remapping in hippocampal regions, but not the subiculum. Relative to controls (no cue alterations), alteration of wall patterns elicited significant increases in exploratory locomotion through the open field, while combined alterations of floor colour and wall patterns elicited an even higher increase in exploratory locomotion. In addition, combined alterations (floor colour and wall patterns) significantly increased rearing frequency, and significantly decreased the time the rats spent immobile. These findings are relevant to how changes in environmental context affect neuronal responses in the hippocampal formation, and may aid in the development of novelty-response tasks where novelty resides in open field surfaces.

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1. Introduction

The hippocampal formation constructs context-specific representations, which likely underlie its function in context-dependent memory. Making changes to environmental context while recording neuronal activity has produced important insights into neuronal representation in different regions of the hippocampal formation, e.g. [1–12]. Such studies however rarely include observation of behaviours that are responsive to these changes in the environment. Two examples can illustrate why knowledge of global behaviour is useful. The subiculum is remarkably context-insensitive in its spatial coding [6,13], while CA3, CA1, and the dentate gyrus are context-sensitive, and 'remap' in novel/changed environments, e.g. [1–4,7,14]. Without global behavioural data, we cannot know if subicular cells show context-insensitivity simply because the change to the new context lacks ethological salience. Secondly, in conditions where hippocampal cells respond to novel context-change, we must address if and to what extent altered hippocampal responses might be attributable secondarily to the changed behaviours which occur following novelty, rather than primarily to the neuronal responses to novelty *per se*.

Ideally, perhaps, observation of novelty-responsive behaviour should proceed simultaneously with recording of neuronal responses [15,16]. However, combining the two approaches can be complex. More importantly, such combined studies are not necessarily sufficient by themselves. For instance, unit-recording studies use food-deprived rats trained to forage throughout the environment, which likely obscure behavioural responses related to sampling the whole environment. Furthermore, novelty responsiveness may be blunted by motivation to feed. Other typical unit-recording procedures, such as the presence of a nearby human, the use of implanted drives, headstages, cabling and so on, could also dampen certain behaviours. Thus, although obvious caveats apply, some purely behavioural studies are likely important in testing and assessing the validity of brain–behaviour relationships.

A literature on the use of rearranged objects to examine behavioural and hippocampal responses to spatial change, e.g. [16–18], already exists. There have also been important hippocampus-relevant studies on the effects of changing an open field's size and shape [19–21]. Here, we asked if the commonest procedures used to provoke context-sensitive change in hippocampal

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neurons, that is, changing the wall patterns, e.g. [3,6,8,14] and floor colour, e.g. [10,22] of the environment, would elicit behavioural changes.

2. Methods

Subjects were male Lister Hooded rats ($n = 30$), weighing 330–380 g 1 week before testing. They were housed in pairs in under a 12 h light cycle (lights off at 15:00 h). Food and water was available ad libitum except during testing. The experimental environment was a transparent Perspex box with walls 62.5 cm wide and 50 cm high. The arena had removable Perspex flooring in two colours: black and white. The white flooring was ruled over with black pen (many weeks before testing) into 16 equally sized square sections which were used during scoring. Behind the four transparent walls was one of two sets of patterned card (62.5 cm × 50 cm) featuring: (a) alternating black and white stripes (stripes 12.5 cm wide); (b) black background with a white circle (31 cm diameter). The floors and walls were cleaned in between trials using 5% ethanol solution. All trials were recorded using a camera mounted overhead linked to a DVD recorder.

Each subject underwent nine successive trials, each trial lasting 4 min, following the basic design of [23]. All subjects experienced eight habituation trials in which they were exposed to the same floor/wall combination, and then a 'probe' trial. Subjects were randomly assigned to one of three groups ($n = 10$ per group): Control group, which experienced no environmental change in the probe trial, Wall Change group (altered walls in probe trial), and Wall&Floor Change group (altered walls and floors in probe trial). Control subjects experienced eight trials of a white floor and black-and-white striped walls, the Wall Change group experienced a white floor and black walls each featuring a large white circle, and the Wall&Floor Change group experienced a black floor and black walls each featuring a white circle. All groups experienced the same 'probe' trial of a white floor and black-and-white striped walls. Levels of illumination were: 37 lx in the two white-floored configurations (i.e. the probe trial for all three groups, and the baseline environment for Control and Wall Change groups), 35 lx in the black-floored environment (baseline environment for Wall&Floor Change group), and 50 lx in the experimental holding area, where rats were kept for 3 min prior to every trial. Thus, rats could not directly compare the 35 lx and 37 lx configurations; entry to these was always mediated by the (brighter) holding area.

All subjects were weighed and handled for 2 min daily during weeks 1 and 2 prior to testing. On days 4–7 of week 2 each subject was also carried in its home cage from the holding room to the holding area outside the experimental room. The experiment was run over 5 days beginning on day 1 of week 3, with six subjects tested per day. Each day consisted of two experimental sessions (10 a.m. to 1 p.m. and 1.30 p.m. to 4.30 p.m.). Subjects from the three groups were run in a pseudo-random order over the 10 experimental sessions.

Each subject was transferred from their home cage to a transportation cage and carried to the holding area where they remained for 3 min before testing commenced. During this period the experimenters cleaned the environment with 5% ethanol; cleaning occurred before all subsequent trials. The DVD recorder was then set to record, the subject was removed from the transportation cage, carried into the experimental room by one experimenter and placed in the centre of the experimental arena. The experimenter left the room and the 4 min trial began. At the end of the trial, experimenters re-entered the room, replaced the subject in the holding area, and cleaned the environment. After trial 8, the environments were re-configured (cues were removed and replaced for the control group). The inter-trial interval was 3 min. Trial and inter-trial-interval durations were timed by stopwatch.

Behaviour was scored from the DVDs using five observers at two levels of detail. Firstly, trials 1–9 were scored for frequency of rearing and visits to each of the 16 sections. Secondly, using the program Hindsight (Scott Weiss, Leeds University, [24]), the baseline and probe trials (trials 8 and 9) were scored (by BK, JS, AW) for the duration of rearing, grooming and immobility behaviour. A transparent acetate sheet divided into 16 equally sized square sections was placed on the scoring monitor for scoring visits to a square. Subjects were defined as being present only in one section at any time, where the majority of the body was located. Two measures of thigmotaxis were obtained by scoring the visits to, and duration in, the outer 12 squares as a proportion of total visits (thigmotaxis frequency) and total trial time (thigmotaxis duration). Rearing was defined as the subject rising up on its hind legs, and ended when one or both front paws touched the floor again. No distinction was made between rearing away from or against a wall. If a rat proceeded to groom within a second of lifting its front paws, this was not counted as a rear. Grooming was defined as licking/washing of the head and body. Immobility was defined as the absence of locomotion but could include head movements. For scoring purposes, a trial was considered to start one second after the rat was placed into the environment. One Wall Change subject could not be scored due to a recording malfunction. Inter-rater reliability coefficients were obtained by double scoring the same trials, and performing Pearson's correlations on the pairs of scores. This was done for 38% of the data (four Control subjects and three from each of the Wall and Wall&Floor Change groups).

Total visits, and rear frequency over trials 1–8 were analysed using a 3 × 8 between subjects ANOVA. The Welch *F*-value was used when homogeneity assumptions were violated. To obtain the direction and magnitude of the change in each behaviour for each subject in the probe trial (trial 9) relative to the baseline trial (trial 8), a behavioural change index (BCI) was calculated. This index was calculated as $(\text{Probe}^N - \text{Baseline}^N)/(\text{Probe}^N + \text{Baseline}^N)$, and was thus positive (negative) when more (less) of the given behaviour occurred in the probe trial than the baseline trial. One-way ANOVA was conducted on the BCI scores, followed by Bonferroni post hoc tests, or Games Howell post hoc tests when sphericity could not be assumed.

3. Results

Inter-rater Pearsons coefficients were as follows: total visits 0.99; frequency of periphery visits 0.99; periphery duration 0.99; rear frequency 0.86; rear duration 0.98; groom duration 0.97; immobility duration 0.83 (all p values <0.0001).

Total visits into each of the 16 sections showed a reduction for all groups over trials 1–8; indicative of habituation (Fig. 1A). There was a significant effect of trial ($F_{7,168} = 73.13$, $p < 0.0001$), but no significant effect of group ($F_{14,169} = 1.07$, $p = 0.38$). Bonferroni post hoc tests on all possible trial comparisons revealed a significant reduction in visits between trial 1 and all other trials (all $p < 0.0001$), between trial 2 and all other trials except trial 3 (all $p \leq 0.006$), between trial 3 and trials 6–8 (all $p \leq 0.004$), and between 6 and 7 ($p = 0.037$). Rearing frequency declined over trials 1–8 across all

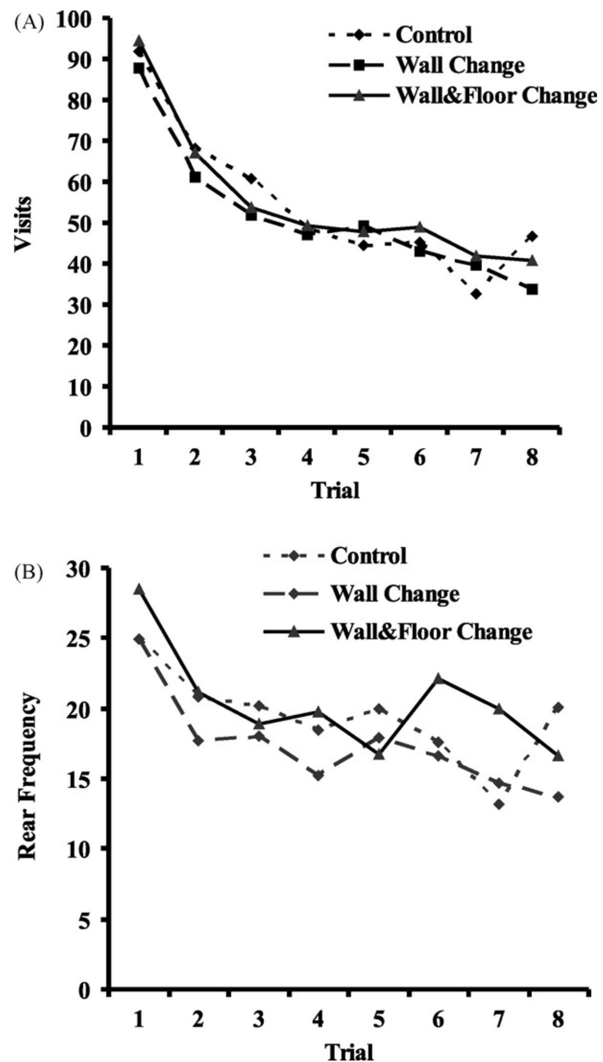

Fig. 1. Total visits (A) and rear frequency (B) decrease with repeated exposure to unchanged environments. Mean of total visits (A) and rear frequency (B) over trials 1–8 for the three groups.

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