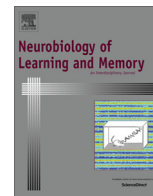




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Conditioning with spatio-temporal patterns: Constraining the contribution of the hippocampus to configural learning



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ABSTRACT

The conditions under which the hippocampus contributes to learning about spatio-temporal configural patterns are not fully established. The aim of Experiments 1–4 was to investigate the impact of hippocampal lesions on learning about where or when a reinforcer would be delivered. In each experiment, the rats received exposure to an identical set of patterns (i.e., spotted + morning, checked + morning, spotted + afternoon and checked + afternoon); and the contexts (Experiment 1), times of day (Experiment 2), or their configuration (Experiments 3 and 4) signalled whether or not a reinforcer would be delivered. The fact that hippocampal damage did not disrupt the formation of simple or configural associations involving spatio-temporal patterns is surprising, and suggests that the contribution of the hippocampus is restricted to mediated learning (or updating) involving spatio-temporal configurations.

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1. Introduction

The hippocampus plays a central role in episodic memory in humans (e.g., [Tulving, 2002](#); [Tulving & Markowitsch, 1998](#)). The suggestion that this role is at least partly conserved in nonhuman animals receives support from a variety of sources (e.g., [Aggleton & Brown, 1999](#); [Eacott & Norman, 2004](#)). For example, [Iordanova, Good, and Honey \(2008\)](#) showed that rats could learn that the whereabouts of two auditory stimuli (a tone and a series of clicks) depended on the combination of the times of day and the contexts in which they were placed. Thus, in the morning a tone was presented in one context (A; a chamber decorated with spotted wallpaper) and clicks were presented in another context (B; a chamber decorated with checked wallpaper); whereas in the afternoon the tone was presented in context B and the clicks in A. The fact that the rats had encoded the four configurations was revealed by pairing the tone with mild shock at midday in a third context (C; an undecorated chamber), and then showing that the rats were more fearful in the context + time of day configurations in which the tone had originally been presented (i.e., context A in the morning and context B in the afternoon). This effect was abolished in rats that had pretraining excitotoxic lesions of the hippocampus, and also by inactivation of the hippocampus during the test ([Iordanova, Burnett, Aggleton, Good, & Honey, 2009](#); see also, [Iordanova, Burnett, Good, & Honey, 2011](#); see also, [Ergorul &](#)

[Eichenbaum, 2004](#); [Li & Chao, 2008](#)). There was no effect of the same manipulations of hippocampal function in simple discriminations where the context (A or B) predicted the nature of the auditory stimulus (irrespective of the time of day), or the time of day indicated which auditory stimulus would be present (irrespective of the context in which rats were placed; for a review, see [Honey, Iordanova, & Good, 2014](#)).

There are alternative theoretical bases for predicting that the hippocampus will play a selective role in learning what will happen where and when. For example, the procedures in which there were deficits were configural in nature: the combination of contexts and times of day was critical to learning where the auditory stimuli would be presented ([O'Reilly & Rudy, 2001](#); [Rudy & Sutherland, 1989, 1995](#); [Sutherland & Rudy, 1989](#); see also, [Alvarado & Rudy, 1995](#)). Also, the nature of the stimuli that need to be combined had clear episodic content (which auditory stimulus was presented where and when; see [Aggleton & Pearce, 2001](#); see also, [Thorpe, Bates, & Wilkie, 2003](#)). However, these analyses apply somewhat less readily to a final observation using this procedure: Disruption of synaptic transmission and NMDA receptor-dependent plasticity processes in the hippocampus during the stage in which the tone was paired with shock (in context C at midday) also abolished the critical effect during the final test; and this manipulation did not affect simple conditioning to the auditory stimuli ([Iordanova, Good, & Honey, 2011](#)). This observation suggests that the hippocampus might be involved in mediated learning ([Hall, 1996](#); [Holland, 1981](#)) involving configurations rather than in configural learning *per se*. According to this analysis, the

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presentation of the tone during aversive conditioning trials evoked the stored configurations involving the tone (i.e., spotted + morning + tone and checked + afternoon + tone) and these evoked memories become linked to the memory of shock. This analysis is consistent with recent investigations of the conditions under which the hippocampus is involved in sensory preconditioning effects involving audio-visual stimuli (Lin, Dumigan, Good, & Honey, 2016; for a review, see Lin & Honey, 2016; see also Wimmer & Shohamy, 2012).

The alternative analyses of the results presented by Iordanova et al. (2009), Iordanova, Burnett, et al. (2011), and Iordanova, Good, et al. (2011) make contrasting predictions about the impact of hippocampal lesions on direct learning about spatio-temporal patterns, in which configurations or their components predict whether a reinforcer will be delivered. If the hippocampus is involved in configural learning or specifically configural learning with spatio-temporal stimuli, then lesions to this structure should result in the same pattern of dissociations that was observed by Iordanova et al. (2009), Iordanova, Burnett, et al. (2011), and Iordanova, Good, et al. (2011). However, if the hippocampus is involved in retrieval-mediated learning involving configural memories (Lin & Honey, 2016; Lin et al., 2016; see also, Lin, Dumigan, Recio, & Honey, 2017; Schlichting & Preston, 2016; Wimmer & Shohamy, 2012) then direct learning involving the same configurations might not be disrupted by hippocampal lesions. The experimental designs employed to assess these predictions are presented in Fig. 1. In Experiments 1 and 2, the context in which animals were placed (spotted or checked) or time of day in which they were placed there (morning or afternoon) predicted the delivery of the reinforcer (food); whereas in Experiments 3 and 4, the combination of context and time of day predicted whether or not a reinforcer (food in Experiment 3 and shock in Experiment 4) would be delivered.

2. Materials and methods

2.1. Animals

Naïve Lister hooded rats were used (*Rattus norvegicus*) in all experiments. Sixteen rats were used in Experiment 1 (supplied by Harlan Olac Ltd, UK; mean weight = 306 g) and Experiment 2 (supplied by Harlan Olac Ltd, UK; mean weight = 317 g). Twenty-seven rats were used in Experiment 3a (supplied by Charles River, UK; mean weight = 454 g); and 32 rats were used in both Experiment 3b (supplied by Harlan Olac, UK; mean weight = 321 g) and

Experiment 4 (supplied by Harlan Olac Ltd, UK; mean weight = 370 g). All rats were maintained at 85% of their *ad libitum* weights by giving them a restricted amount of food at the end of the day (≈ 1830 h). The rats were housed in pairs in a colony room that was illuminated between the hours of 8 a.m. and 8 p.m.; and behavioral training began at, approximately, 09:30 each day.

2.2. Surgery

There were two groups of rats in each of the experiments: Sham and Hpc. In Experiments 1 and 2, there were 8 rats in both groups. In Experiment 3a, there were 13 rats in group Sham and 14 rats in group Hpc; and in Experiments 3b and 4 there were 16 rats in each group. All rats were first anaesthetised using an isoflurane-oxygen mix and then placed in a stereotaxic frame (Kopf Instruments, Tujunga, CA). The bone of the skull above the region to be lesioned was removed, and rats in group Hpc (for Experiments 1–4) were infused with ibotenic acid (Biosearch Technologies, San Rafael, CA; dissolved in phosphate-buffered saline [pH 7.4] to provide a solution with a concentration of 63 mM) through a 2- μ l Hamilton syringe held with a microinjector (Kopf Instruments, Model 5000). Table 1 shows the coordinates where the tip of syringe was positioned relative to bregma and associated volumes that were injected. A total of 15 infusions per hemisphere were made with an infusion rate of 0.05 μ l/min and diffusion time of 2 min. After each injection, the needle was left in position for 2 min to allow diffusion of the ibotenic acid and to limit the spread of the drug into overlying cortical areas. Rats in group Sham received the same surgical preparation with the exception that the dura was perforated with a 25-gauge Microlance3 needle (Becton Dickinson, Drogheda, Ireland), but no fluid was infused into the brain. During recovery, the rats were handled and weighed daily. Food restriction and behavioral testing did not commence for a minimum of 14 days post-surgery when rats had established their preoperative weights.

2.3. Apparatus

Experiments 1–3 were conducted in the apparatus described in Dumigan, Lin, Good, and Honey (Experiment 1; 2015). Briefly the chambers (23.0 cm \times 24.5 cm \times 21.0 cm, L \times W \times H; supplied by Camden Instruments Ltd., UK) were arranged in a 2 \times 2 array, and were constructed from three aluminium walls, an aluminium ceiling, and a plastic wall that served as the door to the chamber. The ceilings and walls of the top pair of boxes in the array were

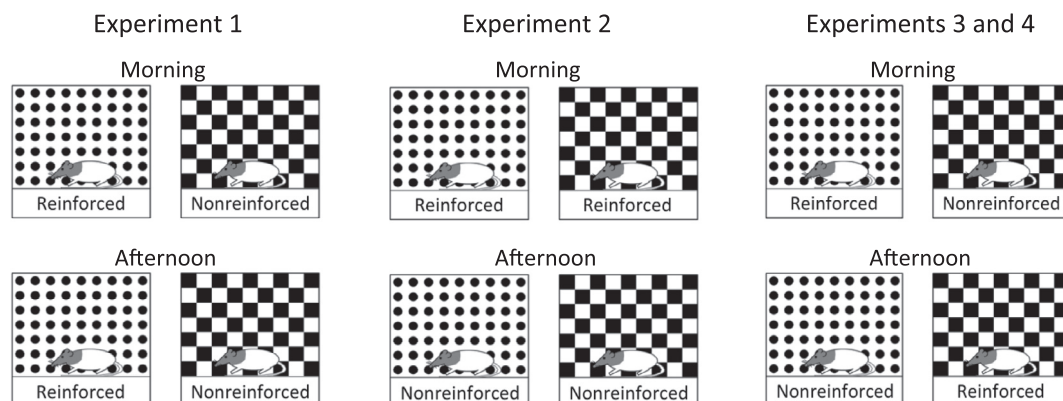


Fig. 1. Schematics for the experimental designs used in Experiments 1–4. All rats received presentations of the same four context + time of day patterns. Whether the patterns would be reinforced or nonreinforced was predicted by the context (spotted or checked; Experiment 1), time of day (morning or afternoon; Experiment 2), or the configuration of context and time of day (Experiments 3 and 4).

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