



Research report

Ontogeny of object-in-context recognition in the rat



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HIGHLIGHTS

- Associative learning of objects and contexts develop prior to weaning in the rat.
- Control tasks confirm that task performance requires associative learning.
- Object-in-context learning in preweanling rats depends on salient proximal cues. When distal cues define the contexts, object-in-context learning is present in juvenile but not preweanling rats.

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ABSTRACT

The object-in-context recognition (OiC) task [19] is a spontaneous exploration task that serves as an index of incidental contextual learning and memory. During the test phase, rats prefer to explore the object mismatched to the testing context based on previous object-context pairings experienced during training. The mechanisms of OiC memory have been explored in adult rats [12,35]; however, little is known about its determinants during development. Thus, the present study examined the ontogeny of the OiC task in preweanling through adolescent rats. We demonstrate that postnatal day (PD) 17, 21, 26, and 31 rats can perform the OiC task (Experiment 1) and that preference for the novel target is eliminated when rats are tested in an alternate context not encountered during training (Experiment 2). Lastly, we show that PD26 but not PD17 rats can perform the OiC task when the training contexts only differed by distal spatial cues (Experiment 3). These data demonstrate for the first time that PD17 rats can acquire and retain short-term OiC memory, which involves associative learning of object and context information. However, we also provide evidence that preweanling rats' ability to utilize certain aspects of a context (*i.e.*, distal spatial cues) in the OiC task is not equivalent to that of their older counterparts. Implications for the development of contextual memory and its related neural substrates are discussed.

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1. Introduction

The development of contextual learning and memory has been attributed to the ontogeny of hippocampal function [1]. It was previously thought that the hippocampus was involved in processing polymodal stimuli associated with a context [2]; however, it is now known that contextual learning can be supported by neural systems separate from the hippocampus in scenarios where the hippocampus has been compromised [3], or when contextual learning is mediated by an elemental associative system that obviates hippocampal function [4,5]. The development of contextual learning and memory processes has been well-defined primarily using fear

conditioning paradigms [1,6–8]; yet, it is unclear whether the previously reported ontogenetic, behavioral, and neural determinants of contextual learning are applicable to other context-dependent learning tasks. Developments in behavioral techniques, such as the novelty-preference paradigm, now allows for the examination of these questions.

In recent decades, the novelty-preference paradigm [9,10] has become increasingly popular in behavioral neuroscience research due to its versatility in examining multiple forms of memory and different brain memory systems. The paradigm is based on rodents' innate preference for novel stimuli in their environments [11], and the many task variants within the paradigm can be used to assess different processes of incidental object, spatial, contextual, and temporal learning and memory [12,13]. Novelty recognition paradigms are advantageous for studying the neurobiology of memory because they typically involve a one-trial training phase, and recognition memory has been shown to emerge during early development [14–17]. In adult rats, variants of this paradigm rely

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on different neural systems [13,18], which makes these tasks particularly useful for investigating neurocognitive development.

Object-in-context recognition (OiC) [19] is a variant of the standard object recognition (OR) task that relies on contextual processing. In this task, rats are consecutively exposed to two pairs of identical objects within two distinct contexts. After a delay, rats are replaced into one of the contexts with both object types present. Rats preferentially explore the object mismatched to the testing context (novel target) based on the previous object-context pairings. The learning of object-context associations in the OiC task is incidental (without reinforcement); thus, research utilizing this task is relevant to other context-dependent incidental learning paradigms like the context preexposure facilitation effect (CPFE) [7,8], which is also used to study memory functions of medial temporal lobe structures including the hippocampus and associated cortices [5].

While other forms of recognition memory such as object recognition (OR) and object location recognition (OL) have been studied ontogenetically, to our knowledge there are no studies of the ontogeny of object-in-context recognition. Performance of the OR task emerges before postnatal day (PD) 17 in the rat [16,17], whereas our lab demonstrated that the OL task, which relies on hippocampal function [12,13,16,20,21], emerges between PD17 and 21 [17]. Likewise, the CPFE, a form of contextual fear conditioning that also requires incidental context learning and the hippocampus [7,22–24], ontogenetically emerges around the same time [7,8, but see 25]. The convergence of these findings and other reports on the development of spatial cognition [26,27] suggest that behavioral performance in the OiC task may have a similar ontogenetic profile, given that similar underlying mechanisms are responsible for OiC memory.

The present study aims to expand the developmental literature on contextual learning and novelty recognition tasks by examining OiC task performance after a short delay in PD17, PD21, PD26, and PD31 rats (Experiment 1). In addition, the present study begins to explore the determinants of object-in-context recognition during development by testing whether processing of object-context associations is necessary for OiC task performance (Experiment 2) and whether distal spatial cues are sufficient to support object-in-context learning (Experiment 3). If the OiC task recruits conjunctive (hippocampal) systems for the processing of contexts, then the ontogenetic profile of the OiC task should resemble those of the OL task [17] and the CPFE [8].

2. Experiment 1: ontogenetic profile of object-in-context recognition

In Experiment 1, we examined the ontogenetic profile of the OiC task by observing task performance in rats aged PD17, 21, 26, and 31. These ages were chosen in order to extend our recent findings on the development of the OR and OL tasks [17,28].

2.1. Materials and methods

2.1.1. Subjects

Animal colony and maintenance have been described in our previous reports [17,28]. Subjects were Long–Evans rats bred and housed in accordance with NIH guidelines at the University of Delaware, Office of Laboratory Animal Medicine (OLAM). Time-bred females were housed in clear polypropylene cages (45 cm × 24 cm × 21 cm) containing standard bedding and *ad libitum* access to food and water. Cages were checked for births during the light cycle (12:12), and the day on which newborn litters were found was designated PD0. On PD2, litters were transported from the breeding facility to the laboratory colony rooms, and on the

following day (PD3), litters were culled to 8 pups (generally 4 males and 4 females) and paw-marked by a subcutaneous injection of nontoxic black ink for identification purposes.

A total of 90 (44 M; 46 F) Long–Evans rats derived from 21 litters were the subjects in Experiment 1. Subjects were assigned to one of four age groups: PD17, PD21, PD26, or PD31. These age designations were based on the day of testing, which varied by a day in the youngest and oldest groups (PD17: PD17 or 18, PD31: PD31 or 32). If same sex littermates were assigned to the same age group, they were placed in different context order groups (see Section 2.1.4) as a counterbalancing measure so that no more than one same sex littermate was assigned to the same age × context order combination. Rats in PD26 and PD31 age groups were weaned and housed by sex with littermates in clear polypropylene cages (45 cm × 24 cm × 17 cm) with *ad lib.* access to food and water on PD21. On PD23 and PD28 (+1 day), rats in age groups PD26 and PD31 were housed individually in smaller, white polypropylene cages (24 cm × 18 cm × 13 cm). Alternatively, rats in PD17 and PD21 groups remained with their dam throughout the study except during habituation and testing sessions when they were placed in the same individual cages for transport to the behavioral testing rooms as PD26 and PD31 rats. These housing procedures are similar to our previous studies which have addressed the (lack of) effect of group versus individual housing or age of weaning on age differences in novelty recognition task performance [17].

2.1.2. Apparatus

The apparatus was adapted from Jablonski et al. [28] and Westbrook et al. [17]. Two circular chambers made of white polyester resin panels and measuring 78.7 cm in diameter, 48.9 cm walls, and elevated 26.7 cm off the floor were configured as two contexts that could be easily distinguished by the rats during testing (Fig. 1A and B). The first arena (Context A) was left unaltered and two local spatial cues—a black “X” and a striped circle—were respectively placed on the north and west walls of the arena out of reach of the rats. In the second arena (Context B), a laminated black-and-white striped poster insert was placed around the walls and a laminated black poster, overlaid by a clear acrylic sheet (76.2 cm diameter) and a circular mesh insert, was placed over the arena’s floor. Additionally, a black “+” and bull’s-eye pattern attached to the walls served as local spatial cues in Context B. Both contexts were located in separate rooms with ample lighting allowing rats to utilize the different distal spatial cues within the rooms. Thus, Context A and Context B were composed of contrasting visual, tactile, and spatial (proximal and distal) features. A camera was mounted on a tripod behind the south wall of both arenas which allowed for digital recording of all experimental sessions (see Section 2.1.5). The stimulus objects (Fig. 2A and B)—a fake green apple and glass jar filled with blue stones—were affixed to the arena floor with reusable Velcro in one of two object configurations (see Fig. 1).

2.1.3. Habituation

Rats were habituated to both contexts during three sessions [17,28]. Sessions 1 and 2 occurred the day prior to the testing session for each age group. The first session began between 08:00 and 12:00 h and the second session began 5 (±1) h later. Session 3 occurred the following morning, 5 (±1) h before the testing session. Prior to each habituation session, rats were handled in the animal housing room for 3 min, weighed, and then carted to the behavioral testing rooms. For all habituation (and testing) sessions, rats were placed in the center of the arena facing the north wall. Rats were allowed to freely explore Context A or Context B devoid of objects for 10 min, with the order of context exposures counterbalanced across rats. Following the first 10 min context exposure, rats were removed for a delay of 3–5 min while the arenas were cleaned with 70% ethanol solution. Immediately following the cleaning period,

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