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Research report

Determinants of novel object and location recognition during development

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HIGHLIGHTS

- Object and spatial novelty recognition is evident around the time of weaning.
- Spatial recognition requires NMDA receptor function in juvenile rats.
- Neonatal alcohol exposure does not impair novel object or spatial recognition.

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ABSTRACT

In the novel object recognition (OR) paradigm, rats are placed in an arena where they encounter two sample objects during a familiarization phase. A few minutes later, they are returned to the same arena and are presented with a familiar object and a novel object. The object location recognition (OL) variant involves the same familiarization procedure but during testing one of the familiar objects is placed in a novel location. Normal adult rats are able to perform both the OR and OL tasks, as indicated by enhanced exploration of the novel vs. the familiar test item. Rats with hippocampal lesions perform the OR but not OL task indicating a role of spatial memory in OL [1]. Recently, these tasks have been used to study the ontogeny of spatial memory but the literature has yielded conflicting results [2,3]. The current experiments add to this literature by: (1) behaviorally characterizing these paradigms in postnatal day (PD) 21, 26 and 31-day-old rats; (2) examining the role of NMDA systems in OR vs. OL; and (3) investigating the effects of neonatal alcohol exposure on both tasks. Results indicate that normal-developing rats are able to perform OR and OL by PD21, with greater novelty exploration in the OR task at each age. Second, memory acquisition in the OR but not OL task requires NMDA receptor function in juvenile rats. Lastly, neonatal alcohol exposure does not disrupt performance in either task. Implications for the ontogeny of incidental spatial learning and its disruption by developmental alcohol exposure are discussed.

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1. Introduction

Previous research concerning the developmental emergence of hippocampus-dependent learning and memory has largely focused on reinforcement-driven tasks, such as Pavlovian fear conditioning and appetitive maze learning [4–6]. Typically, performance of the hippocampus-dependent variant emerges later in ontogeny than control tasks that do not require the hippocampus. For example, auditory fear conditioning emerges by postnatal day (PD)16–18, followed by contextual fear conditioning, which emerges around PD23 [4,7–9] and T-maze delayed alternation develops later than position discrimination [5,10]. These findings have been attributed to a delay in hippocampal development and function, which causes spatial learning to develop later than non-spatial forms of learning.

Incidental learning encompasses an animal's natural exploratory tendency when presented with novel environmental stimuli [11,12]. There are spatial and nonspatial variants of incidental learning. The standard object recognition task (OR) includes exposure to two identical objects (sample phase). Following a delay, the animal is presented with a familiar, as well as a novel object (testing phase). The spatial variant, the object location task (OL), is identical to the object version; however, the testing phase includes a familiar object situated in a novel spatial location [1,13–18]. In both cases, preference for the novel object or the object in a novel location is a result of incidental learning occurring during the sample phase and exploratory behavior during the testing phase. One-trial object recognition paradigms provide

Abbreviations: BAC, blood alcohol concentration; CPFE, context preexposure facilitation effect; FASDs, fetal alcohol spectrum disorders; GD, gestational day; NMDAr, NMDA-receptor; OiP, object-in-place task; OL, object location task; OR, object recognition task; PD, postnatal day; SI, sham intubated.

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an opportunity to examine incidental conjunctive processing functions of the hippocampus without the need for repeated conditioning trials or reinforcement contingencies. Incidental learning is thought to be more sensitive than reinforcement-driven learning to disruptions of hippocampal function [12].

Different brain regions contribute to performance of the OR and OL tasks, at least during adulthood. Perirhinal cortex (PER) is required for OR task performance, while the hippocampus (HPC) is required for OL performance [1,15–18]. Studies of the OR task and hippocampal NMDA-receptor (NMDAr) function have produced mixed results, depending on the delay interval between the sample and testing phases [19]. For example, NMDAr antagonists administered either systemically or intrahippocampally prior to acquisition of the OR task disrupts performance with delays ranging from 1 to 24 h [20–23]. However, OR performance remains intact following intra-hippocampal infusions with a 5-min delay between the sample and testing phases [22]. Similarly, intra-perirhinal cortex infusion of AP5 prior to the sample phase impairs OR after a 3 h but not a 5-min delay [24]. Studies in adult rats implicate the role of NMDArs in the OL task [25,26]; however, the effect of NMDAr antagonists in the OR and OL task has, to our knowledge, not been examined during development.

The sensitivity of incidental conjunctive learning to hippocampal injury [12] makes it of great value to study developmental neurobehavioral disorders that involve the hippocampus [27,28]. For example, developmental alcohol exposure produces teratogenic effects in various brain regions, such as the cerebellum and hippocampus [29,30] and impairs neurobehavioral function, including spatial memory in humans [31,32]. Fetal alcohol spectrum disorders (FASDs) affect approximately 2–5 in 100 young children in the U.S. and abroad [33]. In rat models of FASDs, in which alcohol exposure is limited to PD4–9, the third trimester equivalent of human pregnancy, converging neuroanatomical and behavioral evidence reveals hippocampal CA1 [34–36] and CA3 pyramidal cell loss [34]. Ethanol administration restricted to PD7–9 also impairs performance in hippocampus-dependent maze and fear conditioning tasks [37–39], possibly through inhibited induction and transmission of long-term potentiation (LTP) and reduction of hippocampal NMDArs [40–42].

The current report extends previous work from our lab addressing spatial learning and NMDAr function during development and the effect of neonatal alcohol exposure on this function [27,28,43–45]. The OR and OL tasks are being developed here as a probe for examining these issues with incidental learning paradigms. Previous research concerning the developmental emergence of various object recognition paradigms has provided mixed results [2,3] and the developmental role of NMDArs in the non-spatial OR and spatial OL tasks has not been examined. Recent findings from our lab demonstrate that PD7-9 ethanol administration impairs performance of a contextual fear conditioning task that involves incidental learning [27]. Thus, the OR and/or the OL tasks may provide converging evidence for incidental learning deficits as a function of developmental alcohol exposure.

In summary, the purpose of this study was to examine the effects of age, NMDAr antagonists, and neonatal alcohol on OR and OL in juvenile rats. Experiment 1 evaluated the ability of normally-developing weanling and juvenile rats to perform both tasks. The amount of habituation to the empty chamber was manipulated in order to determine how much exposure to the spatial environment was optimal for task performance. Experiment 2 determined whether or not antagonism of NMDArs would impair performance in either or both of these tasks. Based on prior studies with systemically administered MK-801 in spatial learning tasks, we predicted administration prior to acquisition would impair the OL, but not the OR task. Finally, Experiment 3 examined the effects of neonatal alcohol exposure with a dose and window of administration found to be effective in disrupting hippocampal-dependent forms of learning.

2. Experiment 1A: behavioral determinants of developmental object and spatial location memory

Previous research concerning variations of the OR and OL object recognition paradigms during development has produced mixed results [2,3,46–48], highlighting the need for a more systematic approach for examining these tasks. Thus, Experiment 1A sought to compare the OR and OL tasks as a function of empty chamber habituation and sex by using an age during the late stage of postnatal development when performance in these tasks would be expected.

2.1. Materials and methods

2.1.1. Subjects

The subjects were Long–Evans rats bred at the University of Delaware, Office of Laboratory Animal Medicine (OLAM). Time-bred pregnant females were housed in clear polypropylene cages (45 cm × 24 cm × 21 cm) with standard bedding and ad lib. access to food and water. Offspring date of birth was determined by checking for births during the light cycle (12:12) and, if newborn pups were found, that day was designated as PD0. On PD2, litters were transported from the breeding facility to the local animal housing rooms in the laboratory. On PD3, litters were culled to 8 pups (typically, 4 males and 4 females) and were paw-marked by a subcutaneous injection with non-toxic black ink. On PD21, pups were weaned and housed with same-sex littermates in 45 cm × 24 cm × 17 cm cages (except where noted). On PD28 (2 days prior to habituation), rats were individually housed in smaller white polypropylene cages (24 cm × 18 cm × 13 cm) with ad lib. access to food and water for the remainder of the study. Rats were randomly assigned to the OR or OL task. If same sex littermates were assigned to the same task, they were placed in distinct habituation groups (Group 1 vs. Group 3; Habituation Group), so that no more than one same sex pup from the same litter was assigned to any given experimental condition (Task x Habituation Group). When assigning same-sex littermates to experimental groups was unavoidable, data were averaged together and counted as a single observation.

2.1.2. Apparatus

All behavioral procedures were carried out in 1 of two circular arenas measuring 78.7 cm in diameter, with 48.9 cm walls, elevated 26.7 cm from the floor. The arena was constructed of wood with white polyester resin panels constituting the floor and walls. The arena was situated in a well-lit room allowing the rats to see distal visual cues. There were also 2 proximal cues placed inside the top of the wall of the arena; a black 'X' made with electrical tape (10.5 in. × 9 in.; north position) and a circular cross-hatching pattern made from contrasting strips of colored paper (8.5 in. diameter; west position). These cues were situated far enough from the rats to prevent physical contact. Two squares of reusable Velcro (hook component) were attached to the floor of the arena (Velcro USA Inc., Manchester, NH) in order to secure the objects to the arena floor and prevent the rats from displacing them. The relative dimensions and positioning of objects is shown schematically in Fig. 1.

Objects used for exploration were obtained from various sources; however, it was necessary that all objects were easily cleaned and made of nonporous material (Fig. 2). Objects differed in their surface textures, colors and dimensions, yet maintained relative size. The flat base of each object was fully covered with reusable Velcro (loop component). Object C was found to elicit the highest mean spatial

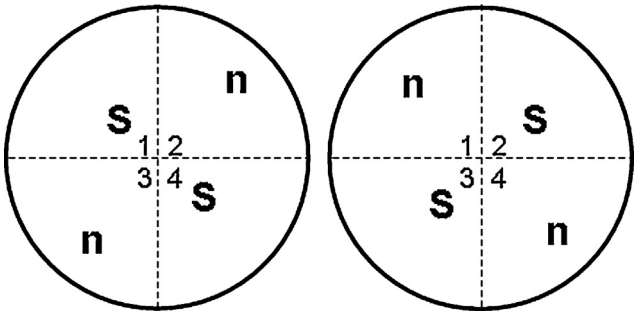

Fig. 1. Relative dimensions. Relative dimensions of the open field arenas for 2 possible combinations of object placement. For the object recognition (OR) task, objects were positioned in standard locations (S) during both the sample and testing phase. For the object location (OL) task, objects were positioned in S for the sample phase. During testing, one object was moved to a novel location (*n*). Quadrants are labeled 1, 2, 3, 4. Configuration 1 (left); configuration 2 (right).

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