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Environmental enrichment reduces impulsivity during appetitive conditioning

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Abstract

Although environmental enrichment is presumed to enhance learning, appetitive behavior may also be altered by this experience: anticipatory responding for sucrose is reduced in environmentally enriched (EE) rats [van der Harst, J.E., Baars, A.M. and Spruijt, B.M. Standard housed rats are more sensitive to rewards than enriched housed rats as reflected by their anticipatory behaviour. Behav Brain Res 2003;142:151–156]. To assess the impact of differential environmental experience on learning and appetitive behavior, we trained 17 EE and socially isolated (SI) rats in a three-phase, operant-shaping procedure for sucrose reinforcement. In phase one, a feeder cue was paired with sucrose availability. In phase two, a nose poke to either one of two lit holes on the opposing wall activated the feeder cue. In phase three, the feeder cue was elicited by a poke to a single lit hole. While acquisition rates in phase one and phase two were similar, EE animals reached phase-three criteria [completion of 100 trials in 45 min and 15 or fewer bad pokes] faster than SI animals. These two groups showed similar session completion rates, reinforced and non-reinforced licking responses, and overall behavioral activity during phase three acquisition; however, SI rats performed more bad pokes (responses to the non-lit hole after nose-poke cue onset) and intertrial interval (ITI) pokes during this training period. Because all ITI (and presumably many bad) pokes were initiated before onset of nose-poke cue, this difference indicates greater anticipatory responding in SI animals. This experience-dependent alteration in appetitive behavior may explain, in part, the tendency of SI rats to show attenuated learning rates in appetitive contexts in which complex contingencies exist.

Keywords: Environmental enrichment; Social isolation; Appetitive conditioning; Sucrose reward; Anticipatory behavior; Rats

1. Introduction

Environmentally enriched (EE) rats show neural and behavioral changes relative to littermates placed in less stimulating, socially isolated (SI) environments [31]. Much of the early work in this literature focused on cortical plasticity (e.g. enhanced gliogenesis, synaptogenesis, dendritic arborization, and increased cortical weight and size) in EE relative to SI animals [2,36,45] and parallel group learning differences [37]. Although environmental enrichment is presumed to enhance learning [31], SI rats consistently show increased locomotion and reduced habituation to an inescapable novel environment relative to EE rats [5,20,21,39] suggesting that SI rats maintain elevated emotionality and arousal [25]. SI animals are also more responsive to incentive stimuli such as drug [4,12] and food reward [18,33–35,39]. Prior to food conditioning, SI animals respond more for non-food "stimulus reinforcement" (tone and light only) suggesting enhanced sensitivity and arousal to environmental stimuli; however, under subsequent food reinforcement, SI bar-pressing rates are proportionally much greater indicating that experience-dependent arousal differences alone do not account fully for increased appetitive behavior in SI rats. Likewise, SI rats show increased anticipatory responding for sucrose reinforcement relative to EE rats [40]. We hypothesize that this elevation in appetitive responding of SI rats slows the process of learning the contingencies of positive reinforcement. To assess the impact of differential environmental experience on learning and appetitive behavior, we analyzed behavioral performance of EE and SI rats during the acquisition of a three-phase shaping procedure for sucrose reinforcement in which the contingencies learned during each subsequent phase were increasingly complex.

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2. Methods and materials

2.1. Subjects

Male Sprague–Dawley rat pups (bred in our colony from animals originating from Harlan Industries, Indianapolis, IN, USA) were cross-fostered to a single mother on postnatal day (p) 2, weaned on p28, and divided equally (with individuals across each group matched for similar weight) into either SI (20 × 24 × 18 cm) or EE (43 × 90 × 46 cm) housing. SI rats were housed individually; EE rats were housed in small groups of 4 or 5. This cross-fostering procedure, which was used to ensure that EE and SI rats experienced similar rearing conditions, was repeated four times resulting in a total of 17 EE and 17 SI rats. The EE cage contained toys, tunnels, and other interactive objects, all of which were repositioned within the cage 3 times/week. To eliminate handling differences, neither group was handled during the experimental housing period; thus, EE rats were not handled during the repositioning of their environment. Animals were maintained on a 12 h light/dark cycle (07:00 lights on) with ad libitum access to food and water. At p45, food (but not water) was restricted to maintain animals at 85% of their free feeding weight for the remainder of the experiment, typically 1–2 weeks after the onset of training. Operant training started on p50. All animal protocols were approved by the Indiana University Institutional Animal Care and Use Committee.

2.2. Behavioral apparatus

A Plexiglas chamber (30 × 30 × 40 cm) containing operant stimuli was positioned within a sound-attenuating compartment. Two nose-poke holes (4 × 3 cm each) were located on one wall; each hole contained a green light-emitting diode (LED) and a photo beam 13 cm above the chamber floor. A lickometer (H24-09R, Coulbourn Instruments, Allentown, PA, USA) was located on the opposing wall consisting of a sipper tube and a photo beam that was mounted on a recessed wall within a 4 × 3 cm opening 13 cm above the floor. Two tone generators (1900 and 4500 Hz), which produced auditory stimuli for the nose poke and feeder cue (see Training protocol below), were attached to the operant chamber 6 cm above the nose-poke holes and the lickometer, respectively. Computer-operated proprietary software (QUNIT, written by T. Bunn and provided by S. Deadwyler, Wake Forest University School of Medicine) automated control of the operant stimuli as well as recorded nose pokes and licks via photo beam breaks.

2.3. Training protocol

All training was conducted with the house lights off. Each animal was exposed to a single, daily training session. Rats were trained in a three-phase shaping procedure for sucrose reinforcement (10% w/v).

The objective of phase one was to prompt licking of the spout in association with the feeder cue. During this phase, a partition blocked access to nose-poke holes on the opposing wall of the chamber. When each rat was placed in the operant chamber, a feeder cue consisting of a tone (three, 300 ms pulses separated by 100 ms, 4500 Hz, 70 dB) and a yellow LED located above the spout was activated. The yellow LED remained illuminated until the rat broke the photo beam located in front of the spout triggering a 1 s release of sucrose (sucrose delivery) followed by a 5 s intertrial interval (ITI). To facilitate association of the feeder cue and sucrose availability, the ITI was increased by 5 s for every 5 trials thereafter. Following 5 trials with a 30 s ITI, phase-one training was complete.

In phase two, the partition covering the nose-poke holes was removed and animals were required to contingently poke lit holes to elicit the feeder cue. When the animal was placed in the operant chamber, an initial, free reinforcement (signaled by feeder cue) was provided. After a 3–8 s ITI, each subsequent trial began with a lit green LED in both nose-poke holes coincident with a 900 ms cue tone (1900 Hz, 70 dB, nose-poke cue). To facilitate poking of a cued nose-poke hole (good poke), two drops of sucrose were placed inside each nose-poke hole (prior to the first session of phase two). The green LED remained lit until a good poke was performed, which was followed by the feeder cue 700 ms later. When the rat broke the photo beam in front of the spout, sucrose delivery was provided. The feeder cue was deactivated with the termination of sucrose delivery and followed by an ITI of 3–8 s. To ensure reward consumption during initial trials of the first session of phase two, sucrose was available for 60 s. After the first 10 reinforced responses, this period was reduced to 15 s. When animals performed 30 trials in 30 min, phase two was complete.

In phase three, only one nose-poke hole was lit (pseudo-randomly selected) at trial onset to stimulate selective responding. After an initial, free reinforcement, the feeder cue was activated 700 ms after good poke. The feeder cue was deactivated with the termination of sucrose delivery and followed by a 3–8 s ITI. After feeder cue onset, sucrose was available for 10 s. Following the first 70 trials, sucrose availability was reduced from 10 to 5 s. Each training session lasted 45 min or 100 trials, whichever occurred first. Phase-three training was concluded once 100 trials were completed in 45 min or less with 15 or fewer bad pokes (pokes to the non-cued hole immediately after nose-poke cue onset).

2.4. Data analysis

To compare the rate of learning in EE and SI rats, we assessed the number of sessions required to reach performance criteria during each phase. To assess what behaviors may have contributed to possible group learning differences, group session averages of good pokes, bad pokes, ITI pokes, total pokes, sucrose-delivery licks, ITI licks, post-trial onset licks, total licks, and total trials were compared. For each comparison, *t*-tests were used to evaluate EE–SI differences.

3. Results

All rats received a single drop of sucrose from the spout during each reinforced trial (~0.13 ml/trial) of each session in