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Research report

Increased behavioral output but intact goal-directed and habitual responding for food reward following early-life social deprivation in rats

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HIGHLIGHTS

- Early social deprivation in rats enhances responsiveness to conditioned reward cues.
- We examined whether instrumental and habitual conditioned responding to reward are also affected.
- Early social deprivation did not alter conditioned instrumental and habitual responding.
- Early social deprivation increased the expression of extraneous un-reinforced behaviors.
- Results shed light on aspects of appetitive conditioning selectively affected by deprivation.

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ABSTRACT

Early-life social adversity, such as child neglect and institutionalized rearing, is associated with later-life difficulties of inhibitory control that may reflect altered attribution of salience to external stimuli. Studies in rats demonstrate that early-life social deprivation results in enhanced responsiveness to reward stimuli and conditioned reward cues. This study examined whether these effects are related to fundamental changes in appetitive conditioning processes involving instrumental goal-directed and habitual responding for food reward. Rats were reared either by the mother (maternal rearing; MR) or in complete isolation from the mother and litter (artificial rearing; AR) and tested as adults in two appetitive conditioning tasks. AR and MR rats did not differ in the amount of goal-directed effort they exerted to obtain food reward on progressive ratio schedules of reinforcement. AR and MR rats also did not differ in the shift from goal-directed to habitual responding on a random interval schedule and they were equally sensitive to changes in reward value. The major difference between AR and MR rats was that AR rats exhibited more non-instrumental responses (empty food magazine entries, ineffective lever presses). Thus, early-life social deprivation of rats through AR affects the expression of unreinforced extraneous behaviors when motivational requirements are high, but does not affect conditioned goal-directed and habitual responding to reward. The findings have implications for understanding what aspects of responsiveness to external stimuli may be selectively affected in disorders of inhibition associated with early-life social adversity.

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1. Introduction

Deprivation of social experience during early-life human development, including child neglect or institutionalized rearing, is linked to a number of behavioral disorders in later life. Among these are difficulties of attention, impulse control, disinhibited social interactions, oppositional behavior, and other problems with inhibitory control [1–6]. Comparable lasting effects of early social deprivation have also been demonstrated in other social mammals, including non-human primates and rodents [7–12]. These

Abbreviations: AR, artificial rearing; CRF, continuous reinforcement; CTA, conditioned taste aversion; MR, maternally reared; PND, post-natal day; PR, progressive ratio; RI, random interval; RR, random ratio; RT, random time.

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behavioral consequences of deprivation may be the result of altered attribution of salience to relevant and/or irrelevant external stimuli [13,14]. For instance, studies in rats and monkeys show that disruption of contact with the mother and/or litter in early life affects later-life behavioral responsiveness to reward and cues predicting reward [14–18]. However, these effects may also be related to general alteration in acquisition and/or performance of appetitive conditioning tasks.

There are three fundamental processes involved in conditioned responding to external stimuli [19,20]. One comprises the relationship between a stimulus and an outcome (associative or Pavlovian conditioning), another comprises the relationship between a response and an outcome (instrumental conditioning), and yet another comprises the relationship between a stimulus and a response (habitual responding) [19,20]. We have previously demonstrated that the deprivation of early-life social experience of rats, by way of artificial rearing (AR), enhances the response to Pavlovian conditioned reward stimuli in adulthood [14,17]. In particular, adult AR rats exhibited increased approach to and contact with a lever that was repetitively presented in association with later food delivery into a nearby food magazine. This behavior, called "sign-tracking", occurs despite the fact that there is no causal relationship between the appearance of or contact with the lever and food delivery. By comparison, most adult maternally reared rats repeatedly presented with the same associative stimuli waited until the food was delivered and then consumed it without approaching the lever. This is referred to as "goal-tracking". Overall, the proportion of rats that exhibited sign-tracking was increased substantially by AR [14]. The goal of the current study was to examine the effects of early social deprivation on the regulation of behavioral responding to reward stimuli in the context of the other two conditioning processes involving instrumental and habitual responding.

In instrumental conditioning, behavioral responding to reward stimuli can be mediated either by goal-directed or habitual responding depending on the schedule of reinforcement used [21–23]. The acquisition of instrumental conditioning reflects the expectation of a rewarding outcome, resulting in responding that is goal-directed. Maintenance of instrumental responding under ratio schedules of reinforcement, where the rate of responding is directly tied to the rate of outcome delivery, elicits a goal-directed pattern of behavior [21]. Conversely, maintenance of instrumental responding under interval schedules of reinforcement, where outcome delivery is constrained by time rather than by the rate of responding, results in the progression of goal-directed behavior toward a habitual pattern of behavior over successive sessions [21]. Here the environmental context in which an outcome is typically obtained promotes behavioral responses, which eventually become independent of the rewarding value of the outcome itself.

We examined the effects of AR on conditioned goal-directed and habitual responding in two experiments. In the first experiment, goal-directed instrumental responding was examined on a progressive ratio (PR) schedule of reinforcement, where increasingly more effort is required to obtain reward [24–26]. The level of persistence in responding on this schedule reflects the motivational properties of the outcome [24,27]. In the second experiment, instrumental responding was assessed on a random interval (RI) schedule of reinforcement, which typically leads to habitual responding over successive training sessions [22,28,29]. We found that AR rats were not different from control rats in the acquisition and maintenance of goal-directed or habitual responding, but differed in the amount of unreinforced and/or extraneous behavior they exhibited when the motivational requirements of the instrumental task were high.

2. Experiment 1 – Goal-directed responding

2.1. Methods

2.1.1. Subjects

The subjects were 24 male Sprague-Dawley rats born at the University of Toronto at Mississauga (UTM) vivarium. They were the offspring of 12 dams obtained from Charles River (St. Constant, Quebec, Canada) and mated at the UTM vivarium. After mating dams were housed individually in clear Plexiglas cages (L 43 cm × W 22 cm × H 21 cm), lined with woodchip bedding ("Beta Chip", NEPCO) with free access to water and lab chow ("5012 Rat Diet", PMI Inc). Housing rooms were maintained at a 22 ± 1 °C and 40–50% humidity. Lights were off between 2000 and 0800 h. All procedures were performed in accordance with the guidelines set by the Canadian Council on Animal Care and were approved by the UTM Local Animal Care Committee.

2.1.2. Rearing conditions

The AR approach was chosen for these studies as it enables the manipulation of the social interactions of developing rats without compromising the provision of nutrition and warmth [30,31].

On the day of parturition (post-natal day – PND 0) litters were culled to 12 pups (~7 males and 5 females). On PND 5 two male pups from each litter were removed, underwent cheek cannulation and were reared artificially thereafter [32]. The remaining pups were left with the mother and litter and were undisturbed until weaning, except for weekly cage changes. At the time of weaning, two male pups were selected from each litter to form the maternally reared control group. Half of the pups from the AR condition ($n = 12$) and half from the maternal rearing condition (MR; $n = 12$) were used in the current experiment and the remaining pups were allocated to an unrelated experiment. One of the AR rats allocated to the current experiment died prior to the start of behavioral testing.

The cannulation procedure was previously described elsewhere [32]. Briefly, the procedure was performed following topical anesthesia of the cheek with lidocaine (EMLA). A small cannula composed of polyethylene tubing (PE10; Clay Adams, Parsippany, NJ) was inserted through the cheek and held in place with plastic washers and a small amount of super glue. Antibacterial cream (Polysporin) was applied at the site of penetration. The entire cannulation procedure took no longer than 5 min. Each AR pup was housed individually in a plastic cup (11 cm in diameter × 15 cm deep) lined with corn-cob bedding (Bed O'Cobs). The cups floated in a temperature controlled water bath (36 ± 1 °C). The tops of the cups were open to allow the cheek cannula to be attached to polyethylene (PE 50) tubing that was in turn connected to a syringe. Each syringe was filled with rat milk substitute formula (modified Messer diet; University of Iowa). The syringes were mounted on timer-controlled infusion pumps (Harvard Apparatus Syringe, PHD 2000). The pumps were programmed to deliver the formula for 10 min/h (24 h daily). Feeding via cheek cannulae began 1–2 h after the cannulation procedure. On the first day of AR, pups were fed 33% of the mean body weight with the volume increasing by 2% per day up to 51%. Thus, on the second day pups were fed 35% of the mean body weight, on the third day 37%, and so on. Each morning pups were removed from the cups, weighed, and had their cheek cannulae flushed with 0.1 ml of sterile water. New syringes were filled with fresh milk and the infusion pumps were programmed according to the pups' new mean weight. Twice per day (morning and evening), each AR pup had its anogenital region stimulated for 30–45 s with a warm, wet, pony-hair paintbrush. This was done to induce urination and defecation.

Feeding via cheek cannulae and tactile stimulation of AR pups ended on PND 17. Each pup was transferred from its cup into an individual small opaque cage (L 27 cm × W 17 cm × H 13 cm) lined

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