

A visual, position-independent instrumental reinforcer devaluation task for rats

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ABSTRACT

Flexible goal-directed behavior has been studied across species using reinforcer devaluation tasks, in which subjects form associations between specific stimuli (cues) and specific reinforcer(s). The reinforcer is subsequently devalued by selective satiation or taste aversion. Following devaluation, subjects adjust their responding to the cues reflecting the new value of the reinforcer. Tasks currently used in rats differ in several ways from tasks used in monkeys and this may explain contrasting results between the two species. To address one of the differences, we developed a rat task independent of spatial cues. It employs two visual cues presented simultaneously, changing left and right positions pseudorandomly. Each cue predicts one of two food reinforcers. Rats were trained to lever press in response to the two visual cues. Subsequently, they were satiated on one of the foods followed by an extinction test where in each trial they could choose to respond to one of the two cues, one predicting the devalued reinforcer and the other the non-devalued. This procedure was repeated later with the alternative food devalued. The rats adjusted their responding by choosing the cue predicting the devalued food significantly less ($p < 0.05$) than the alternative cue. These results show that rats can discriminate two visual stimuli presented simultaneously, devalue two different foods by selective satiation, and transfer the new value to the visual cues. Discrimination of the visual cues is not aided by spatial cues, thereby eliminating a major difference between the instrumental tasks used in rats and the task used in monkeys.

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1. Introduction

Animals depend on the ability to guide behavior in order to achieve specific goals, e.g., outcomes or consequences. Because a behavior that at one time produced a positive outcome, can at a later time produce a negative outcome, it is important to adjust behavior to adapt to changes in consequences. This flexibility allows rapid alterations in behavior in the face of changing outcomes, conferring a survival advantage. This type of flexible goal-directed behavior is enabled by the integration of frontal and limbic neural circuitry.

An example of goal-directed behavior is food seeking. The natural tendency to avoid heavily consumed foods in order to seek relatively novel foods ensures that animals will consume a diversity of foods, thereby increasing the probability of balanced nutritional intake. By extension, a non-edible cue associated with the heavily consumed food changes in value. This process is studied in a

laboratory setting using a “Conditioned Reinforcer Devaluation” task.

Such tasks have been used extensively to study flexible goal-directed behavior in multiple species of laboratory animals (Balleine et al., 2003; Corbit and Balleine, 2005; Hatfield et al., 1996; Izquierdo et al., 2004; Johnson et al., 2009; Malkova et al., 1997; Nelson and Killcross, 2006; Ostlund and Balleine, 2007, 2008; Pickens, 2008; Pickens et al., 2003, 2005). Initial training on these tasks aims to instantiate associations between cues (e.g., a specific object or sound) and specific primary reinforcer(s) (e.g., a specific food or type of juice). A specific primary reinforcer is subsequently “devalued” either by selective satiation (feeding the specific food to satiety) or inducing a taste aversion (causing internal illness following consumption of the specific food). Following devaluation, subjects adjust their responding to the cue in a way that reflects the new “value” of the reinforcer, i.e., they reduce their selection of the cue that predicts devalued reinforcer. The recalibration of the cue does not require additional pairings of the cue with the devalued reinforcer. Instead, the animals must recall which cue predicts the food and integrate that information with the updated value of the food.

The conditioned devaluation sequence described above depends upon the integrity of the basolateral subdivision of the amygdala (BLA) (Balleine et al., 2003; Hatfield et al., 1996; Johnson et al., 2009;

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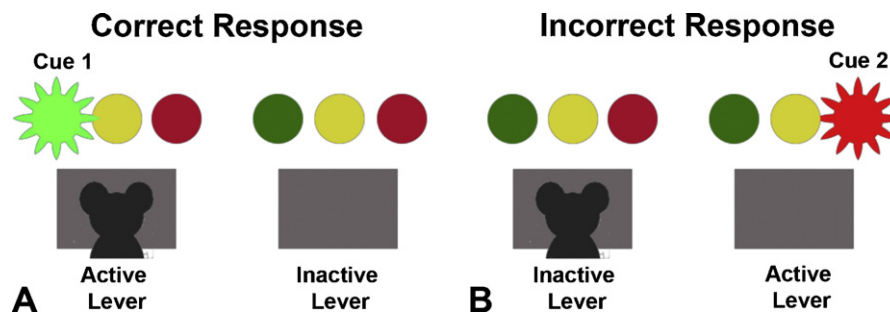


Fig. 1. Phase III: cue training: (A) presentation of Cue 1 (green light) signaled the active lever. A correct response (i.e., pressing the active lever) resulted in the delivery of a food reinforcer (sugar pellet); (B) presentation of Cue 2 (red light) signaled the active lever. Incorrect response (i.e., pressing on the inactive lever) resulted in no food delivery. (For interpretation of the references to color in text, the reader is referred to the web version of the article.)

Malkova et al., 1997; Wellman et al., 2005), the orbitofrontal cortex (OFC) (Izquierdo and Murray, 2004; Izquierdo et al., 2004; Pickens et al., 2003, 2005), the mediodorsal thalamus (MDT) (Izquierdo and Murray, 2010; Mitchell et al., 2007; Ostlund and Balleine, 2008; Pickens, 2008), and the connections between OFC and BLA (Baxter et al., 2000). While each of these neural substrates appears critical for the process, there are inconsistencies across studies with respect to the differential impairment associated with compromised function of amygdala, OFC and MDT (Balleine et al., 2003; Hatfield et al., 1996; Johnson et al., 2009; Malkova et al., 1997; Ostlund and Balleine, 2007, 2008; Pickens, 2008; Pickens et al., 2003, 2005; Wellman et al., 2005).

The neural substrates that are required for conditioned reinforcer devaluation may depend upon the modality of the conditioned reinforcers (e.g., spatial versus non-spatial) and/or the nature of the responses required (i.e., instrumental versus pavlovian). Tasks using distinct types of cues or responses have revealed relationships between task-specific demands and neural substrates (Johnson et al., 2009; Ostlund and Balleine, 2008; Pickens et al., 2003). Currently, we lack an instrumental reinforcer devaluation task for rats that is independent of spatial cues. The ability to resolve the task using spatial cues may be a critical factor that determines the sensitivity to OFC lesions. It is possible that the absence of spatial cues in the reinforcer devaluation task used in monkeys may account for the OFC-dependent nature of conditioned reinforcer devaluation in the monkey, which contrasts the OFC-independent nature of instrumental conditioned reinforcer devaluation in the rat (Izquierdo et al., 2004; Ostlund and Balleine, 2007). In contrast to instrumental tasks, the performance in pavlovian conditioned reinforcer devaluation tasks in rats is dependent on OFC (Gallagher et al., 1999; Pickens et al., 2003, 2005).

Instrumental tasks that have been used to test, conditioned reinforcer devaluation in the rat can be performed using positional cues, e.g., left and right levers (Balleine et al., 2003; Johnson et al., 2009; Ostlund and Balleine, 2007, 2008) whereas the standard task for monkeys requires the use of visual cues only, with position being irrelevant. Because different cortical regions have been implicated in task performance depending on whether the secondary reinforcer is positional or visual (Rushworth et al., 2007a,b), the nature of the cues used in a task are likely to determine behavioral vulnerability to damage of particular structures. For example, OFC, which receives information about stimuli, may be important for reinforcer devaluation tasks when an animal must learn to associate a specific reinforcer with a visual or auditory stimulus, but not with a spatial location (Rushworth et al., 2007a,b).

During the training phase of the standard conditioned reinforcer devaluation task used in monkeys, a series of object discrimination trials are presented; in each trial, one object is baited with a primary reinforcer (food) and the other object is unbaited. Different pairs of objects are presented in each trial. Over the course of

multiple repetitions of the same series of object pairs, the subjects learn to remove the appropriate object to uncover the reinforcer (instrumental action). Half of the reinforced objects in a series are baited with one type of specific reinforcer (e.g., fruitsnack) while the other half of the reinforced objects are baited with an alternative reinforcer (e.g., peanut). The spatial position (left or right) of the reinforced objects is determined according to a pseudorandom sequence. During training, an association is formed between the reinforced objects and the primary reinforcer(s) those objects predict. During a probe session, subjects are presented with a series of trials, offering a choice between two objects. One object predicts one type of primary reinforcer (which has been devalued) and the other object predicts the alternative primary reinforcer. Under baseline conditions, the monkeys switch their preference away from the objects baited with the devalued reinforcer.

The goal of the present study was to design and implement a conditioned reinforcer devaluation task in rats for which spatial cues would be irrelevant. To accomplish this, we incorporated the following characteristics of the standard monkey task: (1) a visual-cue dependent discrimination, (2) instrumental responses to obtain food, and (3) cues independent of spatial position.

Here, we developed a rat task using two visual cues as secondary reinforcers for each of two different foods (primary reinforcers). As in the monkey task, the cues during the probe trial were presented in pairs, changing their left and right positions pseudo-randomly. During the training sessions, rats were trained to press a lever in response to the presentation of a visual cue. In between training and probe sessions, the rats were satiated on one of the two foods. We hypothesized that if the task was successful in detecting devaluation of the cues, the rats would make fewer responses to the cue associated with the devalued reinforcer than to the cue associated with the non-devalued reinforcer.

2. Materials and methods

2.1. Subjects

Behavioral testing was conducted with 32 female Sprague–Dawley rats (Harlan, Indianapolis, Indiana) weighing approximately 250 g at the start of the study. The rats were pair housed in the animal vivarium at Georgetown University Medical Center. The animal rooms were climate controlled and illuminated on a standard light–dark cycle (light on from 6:00 A.M. to 6:00 P.M.). For this study, the rats were food restricted to 85% of their pre-study body weight (10–15 g chow/day) with water available *ad libitum*. Food restriction began 5 days prior to the start of behavioral training and continued throughout training and testing. The study was conducted under a protocol approved by the Georgetown University Animal Care and Use Committee

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