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Research report

Reward uncertainty enhances incentive salience attribution as sign-tracking

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HIGHLIGHTS

- Reward uncertainty is traditionally believed to reduce incentive motivation.
- However, uncertain rewards appear to make predictive cues more attractive.
- As can be seen in the form of increased sign-tracking to uncertain predictive cues.
- It also occurs if certainty about reward prediction is replaced by uncertainty.
- Thus, reward uncertainty is able to enhance the incentive motivational power of CSs.

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ABSTRACT

Conditioned stimuli (CSs) come to act as motivational magnets following repeated association with unconditioned stimuli (UCSs) such as sucrose rewards. By traditional views, the more reliably predictive a Pavlovian CS–UCS association, the more the CS becomes attractive. However, in some cases, less predictability might equal more motivation. Here we examined the effect of introducing uncertainty in CS–UCS association on CS strength as an attractive motivation magnet. In the present study, Experiment 1 assessed the effects of Pavlovian predictability versus uncertainty about reward probability and/or reward magnitude on the acquisition and expression of sign-tracking (ST) and goal-tracking (GT) responses in an autoshaping procedure. Results suggested that uncertainty produced strongest incentive salience expressed as sign-tracking. Experiment 2 examined whether a within-individual temporal shift from certainty to uncertainty conditions could produce a stronger CS motivational magnet when uncertainty began, and found that sign-tracking still increased after the shift. Overall, our results support earlier reports that ST responses become more pronounced in the presence of uncertainty regarding CS–UCS associations, especially when uncertainty combines both probability and magnitude. These results suggest that Pavlovian uncertainty, although diluting predictability, is still able to enhance the incentive motivational power of particular CSs.

1. Introduction

Repeated Pavlovian association between a conditioned stimulus (CS) and an unconditioned stimulus (UCS) increases the predictive value of the CS relative to the UCS, a process that can be described in terms of correlation and computational models such as temporal difference or prediction error models [25,36,38,42,45,46,50]. Most formulations of reinforcement theory do not distinguish between the predictive and incentive values of a cue, so that a CS's incentive value is assumed to depend purely on its predictive value or associative strength, and to become more and more pronounced as the CS–UCS pairings become more reliable [38,50]. The same general principle applies to the patch foraging theory in behavioral ecology – for which animals always tend to optimize the consequences of their actions, and hence exhibit a preference for situations associated with higher reward rates [31,54].

However, there is also evidence that prediction and incentive motivation are not identical [15,48,55,59]. Especially relevant to our current investigation of uncertainty are reports that individuals sometimes display a preference for uncertain rewards rather than for certainty – even when the uncertain option does not provide any advantage in terms of reward rate (e.g. [9,22,28,53]). This suggests that reward uncertainty may be a non-associative source of incentive motivation, just as are deprivation [39], drugs of abuse [47] that potentiate the reactivity of brain mesocorticolimbic systems. All these sources of stimulation share the ability to motivate behavior by means of mesolimbic dopamine, released in the nucleus accumbens from the ventral tegmental area [6]. In particular, there

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is a positive correlation between midbrain dopamine release and the uncertainty of reward delivery in monkeys [18] and humans [34,44]. Also, rats with lesions of the core region of the nucleus accumbens tend to prefer small certain rewards over larger uncertain rewards, while this preference is reversed in the absence of accumbens lesions [11].

Autoshaping is a Pavlovian procedure that is well adapted to assess the motivational magnet strength or attractiveness of a CS that predicts a UCS reward [14,19,21,37,57]. In this procedure, a lever is presented for a short period of time and its retraction is immediately followed by the delivery of a sucrose reward, irrespective of whether the animal engages the lever. Over training, two types of conditioned response develop. Some individuals preferentially display a sign-tracking (ST) response, which consists of appetitive approach and then vigorously nibbling, sniffing, and pressing the lever with consummatory actions that appear closely related to the ingestive sucrose reward. In contrast, other individuals produce a goal-tracking (GT) response, which consists of vigorously approaching the goal dish, and inspecting, nibbling and sniffing the inner location where the reward is delivered. The dopamine antagonist α-flupenthixol in the nucleus accumbens of rats may abolish ST without necessarily affecting GT, suggesting that the ST response especially requires mesolimbic dopamine to develop [19,21,57]. This suggests that ST is a plausible way of indexing incentive motivation.

Regarding uncertainty in autoshaping, Boakes first described in 1977 the surprising finding in rats that a relatively uncertain 50% contingency of partial reinforcement in CS–UCS relationship actually produced higher rates of sign-tracking expressed as CS lever-pressing (and lower goal-tracking) than a fully predictive 100% contingency [9]. Similar reports of finding stronger autoshaping under Pavlovian partial reinforcement than under full 100% reinforcement subsequently appeared also for pigeons (e.g. [12,26]). In the present study, we investigated the effects of uncertainty in rats further, by examining two different types of CS–UCS uncertainty: reward UCS magnitude (e.g., large versus small) and reward probability (e.g. full 100% versus partial or unpredictably varying reinforcement outcome), alone and in combination, on the acquisition and expression of ST and GT responses in an autoshaping procedure (Experiment 1). We also examined the motivational magnet features of the predictive lever CS+ more closely by conducting a detailed videoanalysis of appetitive-consummatory sequences in sign-tracking, consisting of behavioral approach followed by intense ingestive-type nibbles and sniffs directed specifically toward the metal CS+. We also tested the temporal effects of within-individual shifts in certainty to uncertainty (Experiment 2). This study aimed to determine (i) the extent to which different behavioral indicators of ST and GT are affected by the unreliability of the CS in several conditions of reward uncertainty, and (ii) how the sudden occurrence of reward uncertainty after repeated exposure to reward certainty modifies the expression of ST and GT responses.

2. Experiment 1

2.1. Materials and methods

2.1.1. Animals and housing conditions

Female Sprague-Dawley rats ($N = 56$, age: 12–14 weeks old, weight: 150–325 g) were individually housed with ad libitum access to tap water. Rats were handled and partly deprived of food until reaching approximately 85% of free-feeding bodyweight. They were maintained in this deprivation state throughout the experimental procedure. The last two days before the beginning of the training sessions, rats were familiarized with 45-mg sucrose pellets in their home cage. Rats were kept under a reverse 12:12 h light-dark cycle (lights on at 9 p.m.) and constant temperature (21 °C). All experimental procedures were approved by the University Committee on the Use and Care of Animals at the University of Michigan.

2.1.2. Autoshaping chambers

Autoshaping chambers (30 cm × 24 cm × 21 cm) contained two levers (4.5 cm × 2 cm) and a recessed pellet magazine dish (3 cm × 2 cm × 1 cm). The levers were arranged with one on each side of the magazine, which was located in the center of a lateral wall near the floor of the chamber. Each lever had a light at the base that was turned on with its presentation, and an auditory tone (2.9 kHz) was programmed to be produced during lever presentation. An infrared beam and sensor recorded a magazine entry each time the beam was broken. The number of lever presses and magazine entries were recorded using MedPC® software and Med Associates® hardware. The floor, ceiling, and sides of the chambers were made of Plexiglas to allow for video recording. A first camera positioned below the chamber pointed directly upward and a second camera positioned behind the chamber pointed toward the magazine and the two levers. Chambers were placed in cabinets to ensure reduced ambient light and noise. Red LED house lights were mounted to the ceiling and floor of the cabinet and were turned on during the training sessions.

2.1.3. Groups

Rats were divided into four groups ($N = 14$ per group) according to the type of CS–UCS pairings to which they were exposed. Each group was characterized in terms of a probability (100% or 50%) and a magnitude (0, 1, 2 or 3 pellets) of reward delivery per trial.

- 100%-1 (no uncertainty [100% certainty]): rats received one sucrose pellet for each presentation of the lever, that is, a total of 40 pellets per session.
- 50%-2 (probability-based uncertainty): rats received either 2 or 0 pellets with a 50% probability for each lever presentation, that is, on average 40 pellets per session.
- 100%-1–2–3 (magnitude-based uncertainty): rats received 1, 2 or 3 pellets on a random basis (33.3% for each reward amount) for each lever presentation. Here, the animals were exposed to 78–82 pellets per session.
- 50%-1–2–3 (combined probability/magnitude uncertainty): on average, rats received either no pellet with a 50% probability, or 1, 2 or 3 pellets with an equal probability (16.7% for each reward amount) for each lever presentation. The rats obtained a total of 38–42 pellets per session.

2.1.4. Procedure

The day after magazine training – one session of 20 sucrose pellets delivered in the absence of lever presentation – rats started the training sessions under a specific condition of CS–UCS pairings, as mentioned above. Training consisted of one daily session of 40 trials for five consecutive days. Each trial consisted of a presentation of an illuminated lever – located on the right side of the magazine – that became available for 8 s on a variable inter-trial interval (range: 30–90 s) and was accompanied by an auditory tone. The function of the light was the same as that of the tone, forming a compound CS that predicted impending sucrose reward (illuminated lever with tone). The illuminated lever insertion provides a discrete localized and salient object that can become the target of conditioned motivation. The tone further adds to perceptual salience and alerts the rat even when not looking toward the lever location (and causing the rat to immediately orient to the lever). Depending on the experimental condition and/or trial, zero to three sucrose pellets were delivered in the magazine immediately after retraction of the lever. A control lever was constantly available on the left side of the magazine over the sessions. During the sessions, the rats had free access to a tap water dispenser located at the back of the chamber. The number of lever presses and magazine entries was automatically recorded for each session, and the last training session was video recorded for complementary analyses. Rats were returned to their home cage at the end of each session.

2.1.5. Behavioral video scoring

In addition to the automatically recorded number of lever presses and magazine entries, the following behaviors mentioned below were manually counted on the basis of video recordings on training day 5.

- *Look*: head movement toward the lever or magazine without approaching it.
- *Approach*: body (other than head) movement toward the lever or magazine (does not require contact with either the lever or magazine).
- *Lever/Magazine contact*: the lever or magazine was approached to within a distance < 1 cm.
- *Sniff*: small amplitude, short duration exploratory movement of the lever or magazine with the nose, making little or limited contact.
- *Nibble*: small amplitude, short duration exploratory movement of the lever or magazine with the mouth, making contact.
- *Slow bite* (lever *only*): orally grasping the lever between their mandibles.
- *Slow dive* (magazine *only*): insertion of the nose and mouth into the food cup, as would normally occur when retrieving a sucrose pellet.
- *Time latency before lever/magazine contact*: time elapsed before reaching the lever or magazine once the lever became available.