



Research report

Initial uncertainty in Pavlovian reward prediction persistently elevates incentive salience and extends sign-tracking to normally unattractive cues



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HIGHLIGHTS

- Reward uncertainty elevates the attraction of multiple predictive cues.
- Reward uncertainty also recruits non-preferred exposed and distal cues.
- Incentive salience attribution remains persistently enhanced by initial uncertainty.
- Uncertainty directs motivation toward cues and away from reward itself.

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ABSTRACT

Uncertainty is a component of many gambling games and may play a role in incentive motivation and cue attraction. Uncertainty can increase the attractiveness for predictors of reward in the Pavlovian procedure of autoshaping, visible as enhanced sign-tracking (or approach and nibbles) by rats of a metal lever whose sudden appearance acts as a conditioned stimulus (CS+) to predict sucrose pellets as an unconditioned stimulus (UCS). Here we examined how reward uncertainty might enhance incentive salience as sign-tracking both in intensity and by broadening the range of attractive CS+s. We also examined whether initially induced uncertainty enhancements of CS+ attraction can endure beyond uncertainty itself, and persist even when Pavlovian prediction becomes 100% certain. Our results show that uncertainty can broaden incentive salience attribution to make CS cues attractive that would otherwise not be (either because they are too distal from reward or too risky to normally attract sign-tracking). In addition, uncertainty enhancement of CS+ incentive salience, once induced by initial exposure, persisted even when Pavlovian CS–UCS correlations later rose toward 100% certainty in prediction. Persistence suggests an enduring incentive motivation enhancement potentially relevant to gambling, which in some ways resembles incentive-sensitization. Higher motivation to uncertain CS+s leads to more potent attraction to these cues when they predict the delivery of uncertain rewards. In humans, those cues might possibly include the sights and sounds associated with gambling, which contribute a major component of the play immersion experienced by problematic gamblers.

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1. Introduction

Gambling addiction has become an increasing burden on American society, and possibly worsened by the widespread introduction of video and online gambling [1]. One of the key features that

makes games so fun to play and gambling so potentially addictive is uncertainty [2]. In gambling, uncertainty is conveyed through low reliability between the lights and sounds (cues) associated with playing and the winning outcome that they predict. Typically, cues that predict reward will attract attention and therefore are more likely to induce cue-directed behaviors, and the attraction in gambling can outweigh any appraisal that overall odds are against the player. For this reason, cue lights and sounds can become powerfully motivating to a gambler. For example, college students expressed increased craving to gamble

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when presented with visual cues or imagery associated with gambling [3].

Autoshaping is a Pavlovian conditioning phenomenon that captures the incentive salience attraction attributed to predictive cues even in animals. Incentive salience attribution transforms such cues into motivational magnets. In autoshaping, a metal lever emerges from a wall for several seconds, serving as a conditioned stimulus (CS) to predict an immediately subsequent presentation of a rewarding unconditioned stimulus (UCS) such as palatable food. Although no instrumental action is required to earn the UCS presentation, rats do not passively sit and wait for the food [4,5]. Instead, some individuals become sign-trackers as the CS–UCS association is learned, approaching and vigorously sniffing, nibbling, biting, grabbing and consequently pressing the CS+ lever that predicts reward. Other individuals become goal-trackers, equally triggered by CS+ presentation, but directing their approach, sniffs and nibbles to the physical location or goal dish where the sucrose reward actually appears. The goal dish is minimally predictive of UCS (being present both during UCS delivery and absence) but maximally proximal to UCS (close in space and time to reward receipt), whereas the CS+ lever is maximally predictive as a discrete event highly correlated with UCS delivery, but is more distal to the physical UCS pellet. Finally, some other individuals show comparable amounts of both behavior types, and are considered to be intermediates [6–8]. Motivational attraction to the Pavlovian cues reflects the amount of incentive salience attributed to that cue, and attraction to the discrete predictive CS+ in particular has been suggested to reflect increased susceptibility to addictive behavior and disorders of impulse control [6,9,10].

Traditionally in learning theory, the incentive value of a CS varies with its associative correlation (predictive value) to UCS prediction [11,12]. Thus a 100% certain CS predictor has maximum predictive strength [13], and should have highest incentive value. However, there is evidence that the incentive and predictive components of a learned reward predictor can be dissociated [14]. For example, pharmacological/physiological manipulations of mesolimbic dopamine levels in the nucleus accumbens alter the incentive, but not the predictive, value of a CS in a reversible fashion [8,15–17]. Furthermore, prediction certainty of a Pavlovian CS may in some circumstances detach from incentive value. A CS that predicts UCS with 100% correlation is highly certain, whereas a different CS that predicts reward with a probability of only 50% would be highly uncertain. There is evidence to suggest that under similar conditions of reward uncertainty, rats as well as humans, sometimes tend to more often approach and work harder for rewards whose delivery is uncertain (i.e., impossible to predict) rather than for rewards obtained with certainty [4,18–24]. Regarding sign-tracking specifically, we showed in a previous autoshaping study that an uncertain CS+ (i.e., 50% of trials rewarded) that predicts a varying and uncertain magnitude of UCS reward (i.e., UCS was either 1, 2 or 3 sucrose pellets on a random basis) could attract more approaches and nibbles than a CS+ that predicted reward with 100% certainty [25]. In other words, there was greater incentive salience attribution to the uncertain CS+, which might or might not be rewarded on any given trial (and if so, with uncertain magnitude of reward) than to the more certain CS that always predicted reward. This indicates that uncertain cues for rewards, although less predictive than cues for certain rewards, can possess greater incentive salience – a result in accordance with the findings that the predictive and the incentive components of reward rely on two distinct processes. At a neuronal level, there is evidence to suggest that reward uncertainty can enhance extracellular dopamine levels in nucleus accumbens [26], and sign-tracking also involves a greater dopaminergic response [5,6,9]. Human pathological gambling also has been related to striatal dopamine [27], and compulsive gambling severity is associated with larger dopamine responses [28].

The above suggests that reward uncertainty is a source of incentive motivation, and that uncertainty motivation can be studied in animals by means of sign-tracking. The present study investigates whether the motivating power of uncertainty can actually extend incentive value to cues that are normally not attractive. In addition, we also aimed to assess whether CS+ incentive enhancement by uncertainty could persist beyond the termination of uncertain conditions, and appear subsequently even if reward prediction became 100% certain. Persistence could be relevant to long-term motivational effects that might contribute to compulsive gambling, which is known to depend (at least, in part) on dysregulation of the dopaminergic control of motivated behavior [29].

2. Experiment 1

This experiment aimed to determine (a) whether uncertain rewards can persistently hold a rats' interest despite a reduction in uncertainty and (b) whether reward uncertainty would assign greater incentive value (sign-tracking) to cues normally not preferred. For example, previous studies have shown that pigeons will choose to consistently sign-track when the CS is close to the location of the UCS delivery or goal, but goal-track when the CS is further away from that location [30], suggesting that distal cues normally do not acquire much if any incentive salience. In addition, previous pilot studies in the lab had shown an apparent spontaneous preference for the more sheltered (less exposed) of two equally proximal cues. As previously [25], we used a combination of a 50% probability and variable magnitude in order to induce uncertainty, but here we also incorporated location uncertainty: rats did not know which lever – among three possible – would be presented on a given trial.

2.1. Materials and methods

2.1.1. Animals and housing conditions

Female Sprague–Dawley rats ($N=24$; 110–150 days old) were bred and reared by the research group from animals purchased from Harlan. Animals were weaned at 21 days of age and housed (cage: 25 × 45 × 20 in.) in groups of 2–3 animals (by gender) with possible litter effects controlled for by randomizing litter assignment across groups, with only a few animals from each litter being assigned to any one group. Shortly prior to the start of the experiment, rats were food restricted (15–20 g of Purina lab chow per rat per day) until reaching approximately 90% of free-feeding body-weight. Rats were housed under a reverse 12:12 h light–dark cycle (light on at 9 pm) at about 21 °C. They had ad libitum access to tap water for the duration of the experiment. All experimental procedures were approved by the University Committee on the Use and Care of Animals at the University of Michigan.

2.1.2. Apparatus

Autoshaping chambers (30 cm × 24 cm × 21 cm) contained four levers (4.5 cm × 2 cm) and a recessed sucrose pellet dish (3 cm × 2 cm × 1 cm). The dish was located in the center of the front wall near to the floor of the chamber. It contained an infrared beam and sensor that recorded an entry each time the beam was broken. Two levers were located on the same (front) wall of the box that contained the sucrose delivery dish or CS goal: one on each side of the dish, and therefore both levers were proximal to the goal dish. Two additional levers were on the opposite or back wall, positioned to mirror the front wall levers, but more distal to the CS goal being separated by 30 cm of open space. Further, one of the two proximal levers, and one of the two distal levers, were positioned near the side door that when open exposed the external room, and through which an experimenter's hand retrieved the rat at the end of trials. The other proximal and other distal levers were further inside the chamber away from the door,

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