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BRIEF REPORT

# Evidence for Motivational Enhancement of Sign-Tracking Behavior Under Reward Uncertainty

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Reward uncertainty has been shown to invigorate rather than attenuate cue attraction and responding. For example, a number of findings have shown that partial reinforcement in autoshaping increases response rates to a conditioned stimulus (conditional stimulus) in comparison with continuous reinforcement. However, identifying the nature of this effect remains a topical question. The frustration theory posits that animals are frustrated by reward loss and predicts that enhanced responding results from higher response rates to conditional stimulus presentations that follow nonrewarded trials rather than rewarded trials. In contrast, the incentive hope hypothesis suggests that animals are motivated by possible future rewards and predicts similar response rates after rewarded and nonrewarded trials. Our results, which consist of a reanalysis of previously published data (Hellberg, Levit, & Robinson, 2018), are consistent with the incentive hope hypothesis because no differences were found between trials that follow rewarded or nonrewarded trials, or between trials that follow small or larger amounts of food reward in rats. There was also no evidence for an accumulation of frustration across each training session, with rats instead displaying enhanced yet stable responding from beginning to end. The incentive hope hypothesis is also briefly discussed in relation to the concept of incentive salience.

*Keywords:* autoshaping, sign tracking, reward uncertainty, incentive motivation, frustration



Autoshaping is a Pavlovian procedure that typically consists of the brief presentation of a conditioned stimulus (CS; e.g., a metal lever) followed by automatic delivery of an unconditioned stimulus (e.g., a food pellet). After repeated trials, two phenotypes emerge during the CS presentations: some individuals approach and interact with the CS (sign tracking), whereas others approach and inspect the food dish in which the food is to be delivered (goal tracking). Only sign-tracking responses—measured as lever presses—will be addressed here. We are interested in the well-established fact that when termination of the CS is followed by food or no food on a random basis (reward uncertainty/partial reinforcement), sign-tracking responses often reach a higher asymptotic value than when it is consistently followed by food (reward certainty/continuous reinforcement) (Anselme, Robinson, & Berridge, 2013; Collins & Pearce, 1985; Glueck, Torres, & Papini, 2018; Gottlieb, 2006; Robinson, Anselme, Fischer, & Berridge, 2014). This partial reinforcement acquisition effect (PRAE) was first reported in a runway procedure (Amsel & Roussel, 1952; Goodrich, 1959; Haggard, 1959). Several hypotheses have been formulated to explain the PRAE, but its very nature remains controversial (Anselme, 2015; Hug & Amsel, 1969; Pearce & Hall, 1980). In particular, it is unclear whether the PRAE is due to the frustration resulting from past nonreward (Hug et al., 1969) or due to the animal's motivation for upcoming rewards (Anselme, 2015). Although it is likely that frustration also elicits some form of motivation, possibly because of an aversive psychological component, for clarity here we refer to a frustration-induced motivation as an effect of frustration, in contrast to an animal's motivation for upcoming rewards, which we refer to as motivation. In this short report, we present behavioral evidence that is consistent with the notion that the PRAE is a consequence of motivation rather than frustration.

Here we analyzed how rats respond to a CS presentation when they were rewarded (R) or nonrewarded (NR) on the previous trial. We do not present original data but rather a new analysis of data already published and collected with a different objective (Hellberg et al., 2018). In their article, the authors notably showed that partial reinforcement had enhanced sign-tracking responses in male, but not in female, Sprague-Dawley rats in the control (drug-free) condition. For this reason, we used the data from the males from this control condition only. They received one daily autoshaping session of 36 trials for 10 consecutive days. Each trial

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consisted of the 8-s presentation of a lever CS with an auditory stimulus (tone or white noise, counterbalanced), followed or not by food delivery, depending on reward conditions. Each CS trial was separated by a variable inter-trial interval (ITI) of 45 s (30–60 s). On each trial, the nine rats trained under continuous reinforcement (Certain condition) obtained one sucrose pellet. On each trial, the nine rats trained under partial reinforcement (Uncertain condition) obtained no reward with a 50% probability or one, two, or three sucrose pellets on a random basis with equal probability—a procedure that had already been shown to induce a PRAE (Anselme et al., 2013; Robinson et al., 2014; Robinson, Anselme, Suchomel, & Berridge, 2015). Thus, compared with the certain rats, the uncertain rats received the exact same amount of CS presentations and pellets per session but could not determine in advance what would be received on any trial. We analyzed the sign-tracking responses during the last 4 training days or sessions ($4 \times 36 = 144$ trials, of 360). We targeted late rather than earlier training sessions because the PRAE was well developed for these days and also because the behavioral expression of motivation and frustration may require consolidated learning of the CS–unconditioned stimulus association.

According to Amsel (Amsel, 1958, 1992), frustration is a negative emotion resulting from the violation of reward expectation. Specifically, the loss of an expected reward induces a nonassociative frustration drive that invigorates the dominant response. The frustration that arises from the absence of reward (nonreward) is assumed to have similar effects, independent of its origin (uncertainty, negative contrast, or extinction). In autoshaping under reward uncertainty, the PRAE therefore suggests that a frustration drive invigorates the dominant sign-tracking response—a phenomenon that should occur early rather than late during the CS presentation because anticipatory frustration tends to increase close to the time/location of food delivery and inhibits responding. So the PRAE is less likely to be observed relative to goal entries because anticipatory frustration is high at the end of the trial, causing inhibition of goal-tracking behavior. Within-trial data could not be analyzed here. But results compatible with the frustration theory would be that the increase in sign-tracking responses under partial reinforcement occurs for the CS presentations that follow NR trials (losses) rather than R trials (gains). In addition, according to the frustration theory, responding after R trials should be similar to responding under certain reward conditions (continuous reinforcement). These predictions (greater responding after NR trials, and no difference in responding after R trials compared with certain conditions) are represented in Figure 1A, left. Finally, as the strength of frustration increases in proportion to the number of exposure to nonrewarded trials (Amsel, 1992, p. 43), it should build across the entire daily session. According to this prediction, not necessarily incompatible with the previous one, sign-tracking responses under partial reinforcement would grow across trials in a given session. This prediction is represented in Figure 1B (Frustration Model).

In contrast, the incentive hope hypothesis posits that, under partial reinforcement, the animal is not frustrated by past nonreward but is motivated by future rewards while knowing that nonreward are possible. Specifically, the animal hopes that the presented CS will reliably be associated with food delivery, independent of what was received or not received previously. This nonassociative process is assumed to be motivational because it recruits and boosts incentive salience or wanting (Berridge & Robinson, 1998) in a context in which reward uncertainty is involved—Note that this concept of motivation as cue-triggered attraction is quite the opposite to the aversive drive associated with frustration. However, incentive hope is irreducible to incentive salience for reasons briefly mentioned further (see also Anselme, 2018a). Like the frustration theory, the incentive hope hypothesis predicts invigoration of sign-tracking responses under partial reinforcement and no PRAE with regard to goal tracking—because hope is about CS reliability, not food directly. But contrary to the frustration theory, it predicts similar higher-response rates for CS presentations that follow both R or NR trials across a session (Figure 1A, right) and predicts these higher response rates to remain stable within the entire session (Figure 1B: Motivation Model).

Here repeated-measure and mixed ANOVAs with planned comparisons were used as appropriate to compute the results along with effect sizes (Statistica 13). Bayes factors were calculated to quantify the support for the motivation model over the frustration model in the instance in which the Motivation Model predicts the absence of a significant difference in responding between R and NR trials (Rouder, Morey, Verhagen, Swagman, & Wagenmakers, 2017). The performance of the certain rats was used as an indicator of responses to R trials under frustration so that the difference between the responses to those R trials and that observed for NR trials in uncertain rats represented the frustration model. A Bayes factor of 3 or more can be taken as substantial evidence for frustration theory and 0.33 or less as evidence for the null hypothesis—which is what the incentive hope hypothesis predicts here. In between, the data are assumed to be insensitive to one or the other option. To analyze a possible accumulation of frustration within a session, the 36 trials of a session were divided into four blocks of nine trials and compared. All analyses were two tailed and performed at a level of significance of $p < .05$.

Overall, the results are consistent with the incentive hope hypothesis, rather than the frustration model, because the CS-directed responses after R and NR trials are very similar for all comparisons. An initial omnibus comparison over the 4 days (sessions) of autoshaping indicates that the rats responded more under reward uncertainty than reward certainty, as predicted by both theories (Figure 1C; Group: $F_{[1,430]} = 67.959$, $p = .00$, $\eta_p^2 = 0.14$; Day: $F_{[3,1290]} = 1.346$, $p = .258$, $\eta_p^2 = 0.00$; Group × Day: $F_{[3,1290]} = 3.081$, $p = .026$, $\eta_p^2 = 0.01$). Reward uncertainty increased responding across all 4 days (all $p$'s = .000). As can be seen in Figure 1D, there was no difference in response rates after R and NR trials across days for rats under reward uncertainty ($F_{[7,854]} = 1.126$, $p = .344$, $\eta_p^2 = 0.00$), highlighting the absence of any form of frustration. Crucially, rats under conditions of reward uncertainty increased responding compared with rats under reward certainty, after both R (Group: $F_{[1,331]} = 62.583$, $p = .000$, $\eta_p^2 = 0.16$; Day: $F_{[3,993]} = 1.022$, $p = .382$, $\eta_p^2 = 0.00$; Group × Day: $F_{[3,993]} = 2.234$, $p = .083$, $\eta_p^2 = 0.01$) and NR trials (Group: $F_{[1,331]} = 64.166$, $p = .000$, $\eta_p^2 = 0.16$; Day: $F_{[3,993]} = 0.367$, $p = .777$, $\eta_p^2 = 0.00$; Group × Day: $F_{[3,993]} = 3.926$, $p = .008$, $\eta_p^2 = 0.01$), supporting the notion that incentive hope not only increased responding after NR trials but also did so after R trials. This goes against the prediction of the frustration model that would suggest response rates after R trials that are similar to those of animals

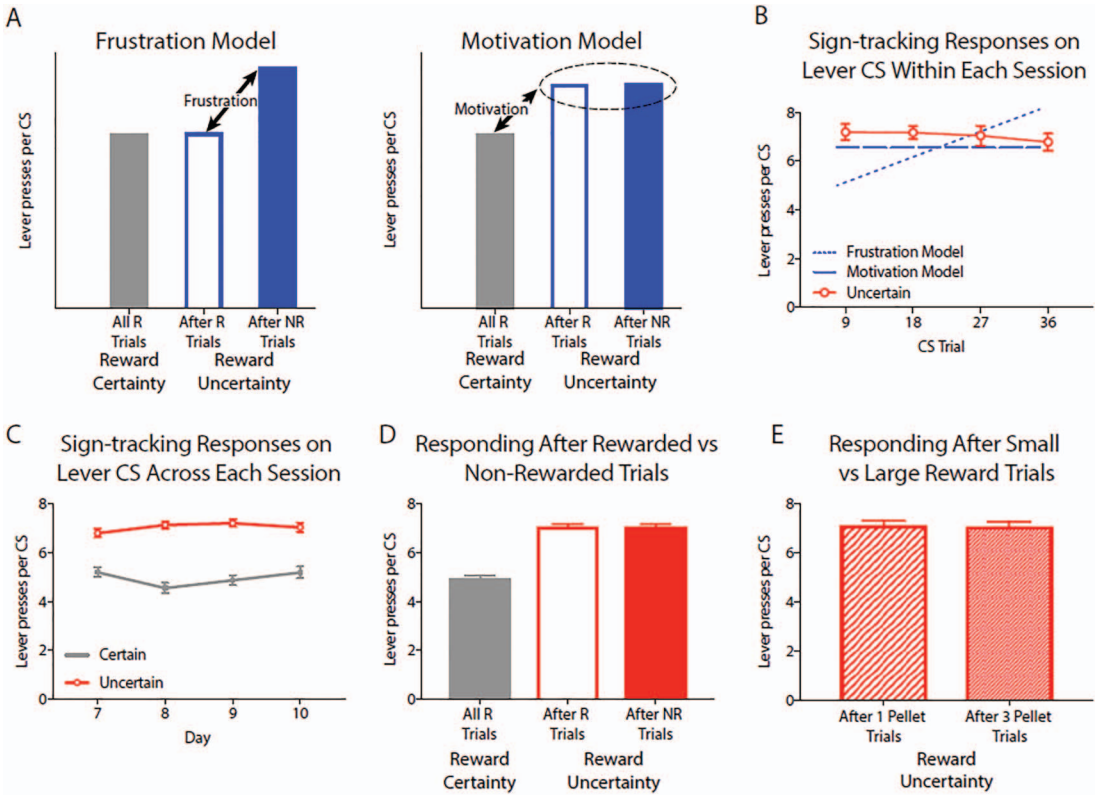


*Figure 1.* Comparison of sign-tracking responses across the last 4 days. (A) Theoretical predictions of frustration theory (left) and the incentive hope hypothesis (right) relative to rewarded (R) and nonrewarded (NR) trials. (B) Theoretical predictions compatible with the frustration theory and the incentive hope hypothesis relative to the accumulation of effects on responding within a training session. Experimental results are also shown. (C) Sign-tracking performance in the form of lever presses per CS presentation of certain and uncertain rats on each day. (D) Overall performance of certain (100%-1) and uncertain rats after R (50%-1–2–3) and NR (50%-0) trials. (E) Overall performance of rats after R trials involving a small reward (one sucrose pellet) or a larger reward (three sucrose pellets). All data are represented as means with standard errors. (The differences between certain and uncertain rats were calculated based on between-subjects data, the other differences on within-subject data). See the online article for the color version of this figure.

experiencing certain reward conditions in which all trials are rewarded.

To determine whether the absence of a difference in responding after R and NR trials was a reliable effect, a Bayes factor was calculated across all days. Here the Bayes factor indicated no overall difference between R and NR trials (K = 0.06), and the daily values remained weak as well (Day 7: K = 0.48, Day 8: K = 0.04, Day 9: K = 0.15, Day 10: K = 0.07).

As noted above, our uncertainty design involved the random delivery of no pellets or of one, two, or three pellets. According to the frustration theory, it would be expected that frustration would be maximal following nonrewarded trials. However, because the rewarded trials varied in the magnitude of the reward, it is possible that even some reward deliveries (in particular for the small reward) were associated with some degree of frustration. It could be argued that the nondiscriminative analysis performed above, in which all rewarded trials were considered together irrespective of reward size, could have camouflaged possible frustration-related effects. If any frustration had developed, it should therefore appear as performance invigoration on trials that follow delivery of one pellet as opposed to trials that follow delivery of the larger three-pellet reward. Again, the results do not support a frustration model interpretation (Figure 1E). Compared with certainty, the rats in the uncertain group responded more to both the small (one pellet; Group: $F_{[1,217]} = 16.527$, $p = .000$, $\eta_p^2 = 0.07$; Day: $F_{[3,651]} = 0.192$, $p = .902$, $\eta_p^2 = 0.00$; Group × Day: $F_{[3,651]} = 2.249$, $p = .081$, $\eta_p^2 = 0.01$) and large (three pellets) reward (Group: $F_{[1,216]} = 11.003$, $p = .001$, $\eta_p^2 = 0.05$; Day: $F_{[3,648]} = 3.271$, $p = .021$, $\eta_p^2 = 0.01$; Group × Day: $F_{[3,648]} = 0.890$, $p = .446$, $\eta_p^2 = 0.00$), and the response rates of uncertain rats were similar following either the small or larger reward across days ($F_{[7,259]} = 1.190$, $p = .309$, $\eta_p^2 = 0.03$).

Finally, the hypothesis of a possible accumulation of frustration as the number of NR trials the animal experienced within a session increased was not confirmed. Figure 1B shows that the overall performance remained stable, and if anything tended to decrease, across the four blocks of nine trials that composed each session across the 4 days ($F_{[3,915]} = 2.131$, $p = .095$, $\eta_p^2 = 0.01$). This result is compatible with the idea that responding is under the

influence of the rats' motivation to respond in the task, rather than any growing frustration.

It should be noted that our effect sizes are rather small. However, this is likely a result from the fact that we used trials rather than sessions as a basis for our calculations. We considered trials because of the necessity to examine and split our within-session data as R and NR trials or as one- and three-pellet trials. If we compare the range of response rates with a CS lever presentation at this level of analysis, strong overlap can be observed between certain (0–16 responses) and uncertain rats (0–17 responses). The group differences exist because the high response rates are infrequent in certain rats and the low response rates are infrequent in uncertain rats. But the presence of extreme responders in both groups is likely to have reduced the effect sizes. The significant interactions are also likely to result from the high values of our trial-based degrees of freedom. Nevertheless, the PRAE was shown after considering the ratio between sign tracking and goal tracking at the session level in the original article (Hellberg et al., 2018).

Collectively, these results are consistent with the idea that the PRAE obtained under reward uncertainty in Pavlovian autoshaping is a consequence of the animal's motivation rather than the animal's frustration. Our findings suggest that the PRAE does not depend on a facilitation of responding to NR, as opposed to R, trials, as some data in line with the frustration theory might have suggested (Dudley & Papini, 1997; Stout, Boughner, & Papini, 2003). It is important to mention that other motivational accounts of performance in uncertainty autoshaping—such as the incentive salience hypothesis (Berridge et al., 1998)—would probably make the same prediction as the incentive hope hypothesis concerning the response rates that follow R and NR trials. However, it has been shown elsewhere (Anselme, 2018a) that the incentive salience hypothesis does not tell us why sign-tracking responses under reward uncertainty are increased (e.g., rather than decreased) compared with reward certainty. It should be noted that sign-tracking responses to a cue have been shown to correlate behaviorally with cue-induced dopaminergic activity (Flagel et al., 2011). In addition, reward uncertainty has been shown to increase dopamine release in response to the cue (Fiorillo, Tobler, & Schultz, 2003; Hart, Clark, & Phillips, 2015), even though these studies did not necessarily provide the animal with the opportunity to express sign tracking. Nevertheless, the incentive salience hypothesis does not provide a rationale for why this increase in dopamine occurs in the first place.

In addition, if incentive salience attribution was just higher under reward uncertainty, this effect should be revealed in appropriate behavioral tests. Preference tests (not carried out here) typically show no preference for uncertainty over certainty, except under specific conditions in which uncertainty is associated with some advantages (Anselme, 2018b; Anselme & Güntürkün, 2019; McDevitt, Dunn, Spetch, & Ludvig, 2016). Also, Robinson and colleagues (Hellberg et al., 2018; Russell & Robinson, 2019) report a similar break point for the certain and uncertain rats in a progressive ratio schedule—in which more responses are required over the trials to get the same reward, a traditional procedure to assess an animal's motivation for that reward (see Hellberg et al., 2018, Figure 4F, left). This suggests that the reward obtained under uncertainty is not more attractive than that obtained under certainty and suggests that the effect of uncertainty is primarily focused on ascribing more value to the cue. Their analysis mixed males and females together, but a reanalysis with males showed only no effect of uncertainty either ($F_{[1,16]} = 0.015$, $p = .905$, $\eta_p^2 = 0.00$). Therefore, the incentive hope hypothesis seems particularly relevant to interpret the present data. Rewards per se are not necessarily more wanted; the individuals simply hope that their predictive CS will be reliable on the ongoing trial. The possible nonreward are what explains the surge of motivational excitement for CSs (because, in nature, more effort is required to find out uncertain food), a process that denotes a survival requirement rather than just greater attraction (for neurobiological details, see Anselme & Güntürkün, 2019). At least in autoshaping, we believe that nonreward is not perceived as a loss because the individuals expect rewards and nonreward with the same probability—causing no specific expectation at the trial level (Anselme, 2015, 2016).

Alternatively, it is possible that frustration takes place in autoshaping on an even smaller scale. Instead of being observable between R and NR trials, the frustration drive could increase responding early in the CS presentation (when anticipatory frustration is relatively low) and decrease it close to the end of the trial (when anticipatory frustration is higher). We have no data available to assess this possibility here. However, our experience with video analysis of uncertain and certain rats in autoshaping suggests that the uncertain rats show stronger lever attraction than certain rats—to the point that they continue to sniff the hole in which the lever has just been retracted. (Gibbon, Farrell, Locurto, Duncan, & Terrace, 1980) found a PRAE in pigeons with a 10-s illuminated key, and they examined the duration of responding during a trial. They reported that "[b]y the end of maintenance training, birds in the low-probability groups showed an accelerated response rate over the trial. High-probability subjects, however, tended to slow their rates of key pecking as the end of the trial approached" (p. 53). Although they observed the reverse pattern about hopper-directed behavior (p. 55), this pattern of responses to the CS appears more compatible with the incentive hope hypothesis than the frustration theory. The incentive hope hypothesis does not say anything about food-related behavior in itself because rats are assumed to hope for CS reliability, not for food directly. So incentive hope is assumed to make the predictive lever more attractive but not food per se, a result reported in our paper and also by Hellberg et al. (2018). We cannot exclude the possibility that an effect compatible with frustration is shown at the very end of the trials, between lever retraction and goal inspection. But the lower reactivity of uncertain rats to pellet delivery could also be due to their longer-lasting attraction to the lever location or simply because of a longer waiting time to hear whether the pellets drop or not.

Why is frustration not shown in autoshaping? One explanation might be that reward uncertainty—at least when rats are not punished and are likely to get reward soon thereafter—is not that aversive and therefore nonreward are ineffective in activating the so-called frustration drive. If correct, adding stressful stimuli (such as loud music) during the training sessions could render rats more irritable, allowing frustration to possibly develop. It would also be important to determine how uncertain rats behave relative to short versus long lever CS presentations (frustration being expected with long CSs; M. R. Papini, per-

sonal communication, 2018) or relative to short versus long ITIs (frustration being expected with shorter ITIs, e.g., Stout et al., 2003). Another explanation might be that, as a Pavlovian process, sign tracking is driven only by the animal's motivation rather than by its representational consequences (Flagel et al., 2011). Indeed, this is a radical difference with instrumental actions, which are controlled by the animal's cognitive representation of their consequences (Dickinson & Balleine, 1994). Because frustration results from the violation of an expected (represented) reward, it should occur only relative to instrumental rather than Pavlovian actions. In support of this view is the evidence that repeated exposure to reward uncertainty in an instrumental design heightens amphetamine-induced locomotion, a stimulus-driven process, but not responses to this instrumental design (Mascia et al., 2019; Singer, Scott-Railton, & Vezina, 2012).

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