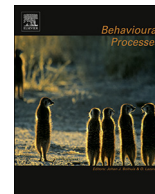




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# Evidence for a shared representation of sequential cues that engage sign-tracking

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## ABSTRACT

Sign-tracking is a phenomenon whereby cues that predict rewards come to acquire their own motivational value (incentive salience) and attract appetitive behavior. Typically, sign-tracking paradigms have used single auditory, visual, or lever cues presented prior to a reward delivery. Yet, real world examples of events often can be predicted by a sequence of cues. We have shown that animals will sign-track to multiple cues presented in temporal sequence, and with time develop a bias in responding toward a reward distal cue over a reward proximal cue. Further, extinction of responding to the reward proximal cue directly decreases responding to the reward distal cue. One possible explanation of this result is that serial cues become representationally linked with one another. Here we provide further support of this by showing that extinction of responding to a reward distal cue directly reduces responding to a reward proximal cue. We suggest that the incentive salience of one cue can influence the incentive salience of the other cue.

## 1. Introduction

Cues in the environment that predict the delivery of reward come to acquire their own motivational value, referred to as incentive salience (Berridge, 2004). The attribution of incentive salience to cues can be manifested in autoshaping or sign-tracking behaviors. For example, when a Pavlovian cue predicts the delivery of reward, animals can develop an appetitive response to the cue itself even though the response carries no causal effect on reward occurrence (Brown and Jenkins, 1968; Jenkins and Moore, 1973). Sign-tracking has unique behavioral properties as it exhibits features not readily explained by typical Pavlovian or instrumental associative learning frameworks. This includes its resistance to associative blocking (Holland et al., 2014) and reward devaluation (De Tommaso et al., 2017; Smedley and Smith, 2018; Nasser et al., 2015; Morrison et al., 2015), its persistence yet flexibility in the face of an instrumental omission contingency (Chang and Smith, 2016; Locurto et al., 1976; Stiers and Silberberg, 1974; Williams and Williams, 1969), and its sensitivity to the cue-reward contiguity and to appetite states (Robinson and Berridge, 2013; Anselme et al., 2013; Smedley and Smith, 2018; Chang, 2014; Vandaele et al., 2017).

Sign-tracking also arises in humans, such as in unnecessary orientation behaviors, appetitive facial electromyography (EMG), skin conductance and increased self-report measures of positive valence and

arousal towards reward predictive stimuli (Wardle et al., 2018; De Tommaso et al., 2017). As excessive drug seeking in addictions is thought to involve heightened motivational valuation of drug-related stimuli, sign-tracking behaviors have arisen as a useful model for understanding how motivation can go awry (Flagel et al., 2009; Tomiet et al., 2008). Despite all of this – its use to access normal and pathological motivation processes, its intriguing behavioral features, and its relevance to human behavior – studies of sign-tracking generally neglect the naturalistic situation where multiple cues for reward occur in a sequence. On this topic, we have shown that sign-tracking behaviors are evoked by a reward distal cue preceding a reward proximal cue preceding an actual reward receipt (Smedley and Smith, 2018). The response rates to the serial cues are comparable to the rates of each cue presented alone. However, in this serial cue condition, response rate tends to be greater on the distal lever as learning progresses (Smedley and Smith, 2018). Extinction of sign-tracking to the reward proximal cue results in an immediate reduction in responding to the reward distal cue, as if the change to the proximal cue informed and updated the response to the distal lever (Smedley and Smith, 2018). Such results are consistent with findings from related studies on Pavlovian audio/visual serial cues (Holland and Ross, 1981; Rescorla, 1979) and instrumental chains (Thrailkill and Bouton, 2015a, 2015b); these studies show that extinction of one cue/action reduces the other, and are thus broadly in line with the notion that stimuli or actions occurring in sequence

Abbreviations: ppm, presses per minute; mepm, magazine entries per minute

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become representationally linked (Holland, 1990; Thraikill and Bouton, 2017b).

It remains unclear whether each lever cue has the ability to mediate responding to the other associated lever in sequence. Our previous result indicated that responding to a distal cue is highly sensitive to the state of the response to the proximal cue, but it is unknown if the reverse would be true as well. Here we address this issue by asking if extinction of the distal cue response leads to a reduction in responding toward the proximal cue.

## 2. Materials & methods

### 2.1. Animals

Long Evans rats obtained from Charles River (N = 16; Charles River, Indianapolis, IN, USA) were single housed in ventilated plastic cages in a climate-controlled colony room on a 12 h light/dark cycle (lights on at 7:00 A.M.). Experiments were conducted during the light cycle. Food and water were available *ad libitum* until 7 days before experimentation. Weight was then restricted to 85% *ad libitum* weight prior and was maintained at this level throughout the experiment to encourage motivated behavior for food consistent prior studies with rats (e.g. Stiers and Silberberg, 1974; Chang et al., 2012; Davey and Cleland, 1982) and birds (e.g. Brown and Jenkins, 1968; Rescorla, 2008). Daily food (Teklad Global 2014: Protein 14%, Fat 4%, Carbohydrates 48%) was provided 1–2 h after each testing session and water was always accessible in the home-cages. All procedures were approved by the Dartmouth College Animal Care and Use Committee.

### 2.2. Apparatus

Experiments were conducted in operant chambers (Med Associates), which were enclosed in sound- and light-attenuating cabinets outfitted with fans for ventilation and white noise. Chambers contained two retractable levers to the left and right of a recessed magazine. Lever deflections were recorded automatically and magazine entries were recorded through breaks in an infrared beam in the magazine.

### 2.3. Sign-tracking

Animals were given a single ~30 min session of magazine training in which grain reward pellets (Bio Serv, Product #F0165, 45 mg dustless precision pellets: Protein 21.3%, Fat 3.8%, Carbohydrate 54.0%) were delivered on a probability schedule of one pellet every 30 s with 60 pellets delivered in the session. 12 daily 60 min sessions of serial lever sign-tracking conditioning then followed. Each session contained 25 presentations of a reward distal lever for 10 s, followed by a reward proximal lever for 10 s, followed by immediate delivery of 2 reward pellets. Intertrial intervals were 120 s. The assignment of right and left levers to reward distal and reward proximal cues were counterbalanced across animals. Following the final conditioning session, animals were pseudorandomly separated into two groups, such that there was no significant difference in responding in training between groups and both left and right lever assignments were balanced between groups (see 3.1). Group Distal Extinction were given non-reinforced presentations of the reward distal lever. Extinction occurred in 5, 60 min training sessions with a total of 250 non-reinforced trials. Group Control was instead placed in operant boxes for the equivalent session length with the same ambient light and fan noise with no programmed experimental events. After this phase, all animals were then presented with the serial lever sequence under extinction in a 60 min, 25 trial session. In a final subsequent session, all animals received a reacquisition test (i.e., in a 60 min, 25 trials) in which the serial lever sequence ended with reward as during training.

### 2.4. Behavioral measures and analyses

Lever deflections and magazine entries were recorded through MedPC. All statistical tests were carried out using R (R Core Team, 2016). Individual linear mixed models (R; “lme4”) were used to analyze effects of dependent variable responding (ex. lever presses per minute (ppm)) by fixed effects of experimental group or lever type (reward proximal or reward distal), and session while accounting for random effects of differences in individual starting values for the dependent variable in session one and differences in individual learning rates over sessions (i.e. random effects). Zero sum contrasts are made for categorical variables (i.e. group and lever type) when appropriate. Linear mixed models are fit by maximum likelihood and t-tests use Satterthwaite approximations of degrees of freedom (R; “lmerMod”). Linear mixed models were analyzed with package lme4 from CRAN (Bates et al., 2015). The reported statistics will include parameter estimates ( $\beta$  values), confidence intervals (95% bootstrapped confidence intervals around dependent variable), and p-values (“lmerTest”, Kuznetsova et al., 2016). Graphs and figures were constructed using GraphPad Prism and Adobe Illustrator.

## 3. Results & discussion

### 3.1. Training

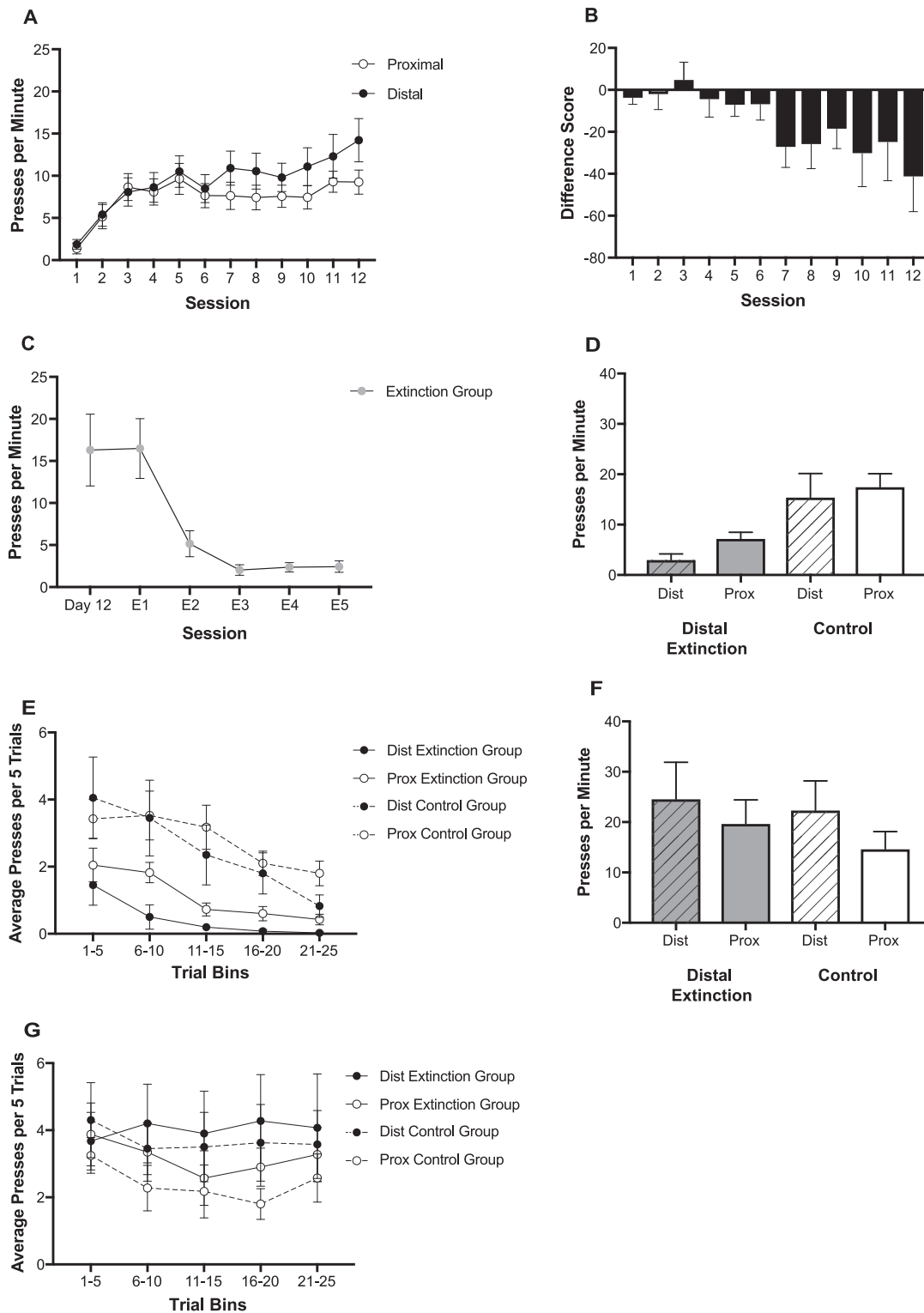
Animals showed a preference, as seen in presses per minute (ppm), towards interacting with the distal lever that developed over sessions (Fig. 1A). This effect, and its magnitude, is consistent with our prior report (Smedley and Smith, 2018). A linear mixed model was constructed of ppm by lever type (distal v. proximal), session of training (1–12), and group (animals destined for distal-lever extinction [Distal Extinction group] and Controls) with random effects of training session (allows for the possibility that animals learn at different rates over time) and animal (allows for the possibility that animals begin training at different rates). The main effect of lever type was not significant (est: -0.868 ppm; CI: -2.60–0.948;  $p = 0.326$ ) nor group (est: -1.16 ppm; CI: -6.15–4.04;  $p = 0.644$ ). The non-significant effect of group indicates that by the end of training, the animals set for the Distal Extinction and Control groups were sign-tracking similarly. There was a main effect of day (est: 0.584 ppm; CI: 0.214–0.882;  $p = 0.005$ ) showing a significant increase in ppm over the training period. An interaction effect of lever type by day (est: 0.424 ppm; CI: 0.177–0.647;  $p = 0.0005$ ) indicated that the distal lever gained nearly 0.5 ppm above the proximal lever over training sessions as well (Fig. 1A). Further, a visualization of differences scores (total proximal presses - total distal presses), averaged for all animals, shows that this distal preference developing over training in the form of negative scores with a mean of -41.4 total press difference on the final day of training (Fig. 1B).

### 3.2. Distal lever extinction

Animals in the Distal Extinction group then underwent 250 non-reinforced presentations of the distal lever cue (i.e. 5, 60 min sessions each with 50 cue presentations) until responding reached minimal levels (Fig. 1C). A linear mixed model including the last session of training as a baseline revealed that the Distal Extinction group dramatically decreased ppm on the distal lever over the 5 days of extinction (est: -3.28 ppm; CI: -6.31–4.16;  $p = 0.006$ ; Fig. 1C). In our previous experiment (Smedley and Smith, 2018), extinction of the proximal lever similarly took 5 days to reach negligible levels of responding. Animals in the Control group were handled and exposed to the task chambers similarly, but no cues were given.

### 3.3. Post-extinction testing (non-reinforced session)

When animals were returned to the serial-cue condition, both



**Fig. 1. Lever Press Responding** All error bars display  $\pm$  SEM (A) Responding in presses per minute toward the distal (black) and proximal (white) levers in training. (B) Difference scores of total proximal presses minus total distal presses calculated for each animal for each session and plotted as an average score per session. Lines projecting above the x-axis represent a positive score indicating proximal lever bias. (C) Extinction of the distal lever within the distal lever extinction group including the last day of training (day 12). (D) Extinction test responding in presses per minute toward the distal (striped) and proximal (solid) levers in training for the Distal Extinction (grey) and Control (white) groups. (E) Average presses per 5 trials in the extinction test on the distal (black) and proximal (white) levers for the Distal Extinction (solid line) and Control (dotted line) groups. (F) Reacquisition test responding in presses per minute toward the distal (striped) and proximal (solid) levers in training for the Distal Extinction (grey) and Control (white) groups. (G) Average presses per 5 trials in the reacquisition test on the distal (black) and proximal (white) levers for the Distal Extinction group (solid line) and Control (dotted line) groups.

groups exhibited an overall decrease in pressing on both levers due to the absence of reward on this extinction test day (Fig. 1D). Over trials within this session, responding to all levers decrease (Fig. 1E). However, critically, the Distal Extinction group showed significantly lower sign-tracking to both lever cues compared to Controls, suggesting that dampening the attraction to the distal cue via extinction had dampened the motivational attraction to the proximal cue as well. A linear mixed model was used to analyze ppm made on each trial by group, lever, and trial (25 trials/session) with random effects of trial and rat. A significant effect of group (est: 1.38 presses; CI: 0.663–2.19;  $p = 0.002$ ) identified that the Distal Extinction group made about 1.4 presses per trial fewer on all levers compared to Controls. There was a non-significant effect of lever (est: 0.179 presses; CI: -0.289-0.680;  $p = 0.445$ ) and non-significant interaction of lever by group (est: -0.356 presses; CI: -0.821-0.079;  $p = 0.108$ ), indicating that neither lever was pressed more than the other in general, and that neither group showed a preference for either lever (Fig. 1D). A significant effect of trial (est: -0.100 presses; CI: -0.145-0.058;  $p = 0.005$ ) showed that animals decreased pressing over the trials in the extinction probe, which was expected given the lack of reward. There was not a significant interaction of lever by trial (est: 0.024 presses; CI: -0.008-0.054;  $p = 0.126$ ) such that all levers decrease pressing over trials equally (Fig. 1E).

### 3.4. Post-extinction testing (reinforced)

When reward was reintroduced to the task in a session following the extinction probe test, all animals rapidly returned to a level of sign-tracking behavior seen during the pre-extinction training (Fig. 1F). A linear mixed model was used to analyze the presses made on each trial by main effects of group, lever, and trial with random effects of trial and rat. A non-significant main effect of group was found (est: -0.012 presses; CI: -2.12–2.18;  $p = 0.991$ ) as well as group by lever interaction (est: -0.445 presses; CI: -1.07–0.148;  $p = 0.150$ ), indicating that neither group differed in overall presses nor in bias toward one lever or another (Fig. 1F). There was a non-significant effect of trial (est: -0.019 presses; CI: -0.050–0.011;  $p = 0.236$ ), nor was there a trial by cue interaction (est: 0.033 presses; CI: -0.012–0.073;  $p = 0.126$ ), indicating that rats did not press differently over trials nor press with a bias toward either lever over trials (Fig. 1G). However, a significant effect of lever (est: 0.626 presses; CI: -0.050–1.24;  $p = 0.049$ ) indicated that over all, regardless of trial or group (see above), rats pressed more toward the distal lever during this reacquisition testing.

### 3.5. Magazine behavior during training and distal extinction sessions

Magazine entry rate over the training period was stable across training sessions (Fig. 2A). A linear mixed model of magazine entries per minute (mepm) over the 12, 60 min sessions by group and session with random effects of session and animal indicates an insignificant main effect of group (est: -2.49 mepm; CI: 8.83–15.0;  $p = 0.259$ ), meaning groups did not differ in their magazine entry rate over training. An insignificant main effect of session (est: 0.129 mepm; CI: -0.76–0.91;  $p = 0.767$ ) indicates that animals maintained similar rates of entry throughout training. Finally, an insignificant group by session interaction (est: -0.038 mepm; CI: -1.25–1.24;  $p = 0.951$ ) indicates that both groups maintained similar rates of entry throughout training.

Analysis of magazine entries over the distal lever extinction sessions shows that both groups do not differ in the rate in which they are decreasingly entering the magazine (Fig. 2B). A linear mixed model of mepm over the last day of training (as a baseline) and 5 days of extinction by fixed effects of group and day shows no main effect of group (est: -1.09 mepm; CI: -11.6–7.40;  $p = 0.829$ ). Both groups significantly decrease entries over sessions with a significant main effect of session (est: -2.11 mepm; CI: -3.58–(-0.759);  $p = 0.013$ ). Interestingly, groups similarly decrease magazine entries as seen in an

insignificant group by session interaction (est: 0.196 mepm; CI: -1.56–2.39;  $p = 0.855$ ).

### 3.6. Magazine behavior during extinction and reacquisition test sessions

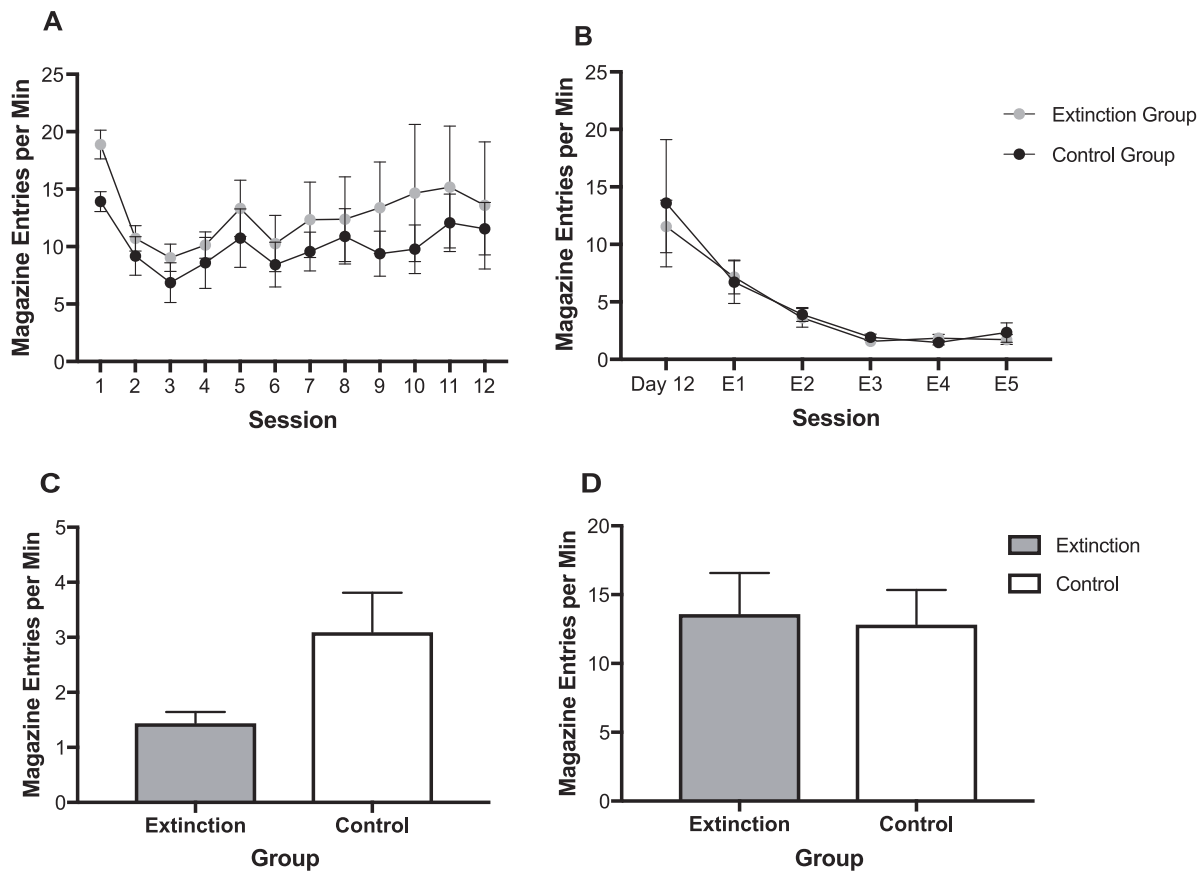
Paired t-tests of total magazine entries during the extinction probe session revealed a significant difference in magazine entries by group ( $t(7) = 2.54$ ,  $p = 0.039$ ), with the Distal Extinction group entering the magazine an average of 86.6 times and the Control group entering 186 times (Fig. 2C). We can conclude that animals that underwent sign-tracking extinction showed fewer magazine entries than animals that received just context exposure, indicating that the non-reinforced presentations of the distal lever did indeed reduce the conditioned food cup response to a greater degree than mere context exposure in test. Notably, this contrast in magazine behavior quickly disappeared upon reacquisition testing where both groups performed similarly with no significant difference in magazine entries ( $t(7) = -0.247$ ,  $p = 0.812$ , Fig. 2D). This supports the notion that the conditioned response of both lever and magazine behavior was rapidly recovered when the reward was returned.

## 4. Conclusion

With presentation of serially occurring lever cues for reward, animals developed a robust sign-tracking response to both cues and a bias towards greater response to the distal cue, similar to a previous report (Smedley and Smith, 2018). The distal cue thus came to capture the most motivational salience; however, the second cue was not treated as redundant and ignored but instead continued to engage motivated responding. Such results are in line with the notion that when cues are available they can engage behavior as opposed to just signaling reward occurrence. This might relate to real-world conditions where sequentially occurring cues support high levels of attraction, maintaining motivation and behavioral approach until a reward is available. The finding that reward distal stimuli carry more incentive value than proximal stimuli may also be relevant to the approach of extinction learning in exposure therapy for disorders related to problematic cue reactivity. If distal cues come to carry considerable motivational impact, then those could be targeted to advantage as well as targeting patient responses to event-proximal cues (e.g., sight of a cigarette or spider).

In this study, following extinction of responding to the distal cue, reduced responding occurred immediately toward the proximal cue in a non-rewarded test session. Magazine entries were lowered during the extinction period in the Distal Extinction group and context-exposed controls. In the non-rewarded test session, entries for Distal Extinction rats remained low but rose again in controls. Once rewards were returned, cue interaction and magazine entry were quickly reacquired. Coupled with the equivalent proximal-extinction result we have reported (Smedley and Smith, 2018), this extinction result indicates that the presence of one serial cue not only elicits a motivational representation of itself, but also of the full cue-cue-magazine/reward sequence. In this view, a mediated learning phenomenon could have occurred (Holland and Wheeler, 2008): the loss of reward pairing with one cue during extinction reduces the reward-relatedness of that cue, but also the value of the other cue as well as of the magazine, leading ultimately to less of a motivational draw from all of the stimuli. A similar relationship between cues/actions has been found in prior Pavlovian and instrumental conditioning studies (Holland and Ross, 1981; Rescorla, 1979; Rashotte et al., 1977; Thraillkill and Bouton, 2015a, 2015b, Holland, 1990; Thraillkill and Bouton, 2017b).

A related explanation is that the lack of a proximal cue and reward during extinction resulted in surprise-related attention to the task, and then attention was high again when sequence was reinstated during the un-rewarded test session. If this added attention to the cues promoted new learning (Wilson et al., 1992; Holland and Gallagher, 1993), then



**Fig. 2.** Magazine entries All error bars display  $\pm$  SEM (A) Magazine entries per minute during training sessions. Groups are graphed separately with Distal Extinction (grey) and Control (white). (B) Magazine entries per minute during the distal extinction sessions with the last session of training (Day 12) as a baseline. Groups are graphed separately with Distal Extinction (grey) and Control (white). (C) Magazine entries per minute in the extinction test session for the Distal Extinction (grey) and Control (white) groups. (D) Magazine entries per minute in the reacquisition test for the Distal Extinction (grey) and Control (white) groups.

that new learning would take the form of reduced sign-tracking (as we observed) because the reward is omitted during this test. Problematic for this interpretation is that reduced sign-tracking cues was evident immediately in the first block of trials (Fig. 2B), and also that animals continued to avoid entering the foodcup in this test (and entered less so than controls). Thus, results appeared not to be due to a within-session enhancement of learning that the serial cues predicted no reward.

Another interpretation is that the cues could be separately associated with reward but not with each other. In this view, during extinction the animals learn that there is no longer food, and as a result any cue associated with the food gets reduced in value. In other words, the results would be the same if we did not pair the serial cues together but rather had them separately associated with the same reward. However, we note that food cup entries went down equivalently in control animals, but in that control group there was not a comparable reduction in sign-tracking. This indicates that what is being lost during distal cue extinction relates to a representation of the distal-proximal-reward relationship and not just separate individual cue-reward relationships. Finally, we acknowledge that we cannot rule out that frustration or disinterest contributed to the extinction results here.

Further work will be necessary to assess if this effect generalizes to other response types and cue modalities (e.g., visual cue interaction). Of note, previous reports (Thrailkill and Bouton, 2015a, 2015b) have found that, using a within-subject design where each subject learns two distinct instrumental chains ( $A \rightarrow B$  and  $C \rightarrow D$ ), extinction of one response ( $B$ ) leads to specific reduction on only the other response within the chain ( $A$ ) and not the other responses ( $C$  or  $D$ ). In this case, we might expect extinction of sign-tracking responses to one cue series (e.g., levers) might not affect sign-tracking to another (e.g., light cues).

Generally, our results highlight the importance of understanding how multiple cues that acquire motivational properties are represented behaviorally and what features underlie that representation.

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The authors have no competing interests to declare.

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