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BRIEF REPORT

Extinction and Spontaneous Recovery of Spatial Behavior in Pigeons

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We investigated extinction and spontaneous recovery of spatial associations using a landmark-based appetitive search task in a touchscreen preparation with pigeons. Four visual landmarks (A, B, C, and D) were separately established as signals of a hidden reinforced target among an 8 × 7 array of potential target locations. The target was located above landmarks (LM) A and C and below B and D. After conditioning, A and B were extinguished. Responding to A and C was assessed on probe tests 2 days following extinction, whereas, B and D were tested 14 days after extinction. We observed spontaneous recovery from spatial extinction following a 14-day, but not a 2-day, postextinction retention interval. Furthermore, by plotting the spatial distribution of responding across the X and Y axes during testing, we found that spontaneous recovery of responding to the target in our task was due to enhanced spatial control (i.e., a change in the overall distribution of responses) following the long delay to testing. These results add spatial extinction and spontaneous recovery to the list of findings supporting the assertion that extinction involves new learning that attenuates the originally acquired response, and that original learning of the spatial relationship between paired events survives extinction.

Keywords: spatial learning, extinction, spontaneous recovery, latent learning

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Although there are many examples of spatial learning, little is known about the acquisition processes that contribute to them. Given the widespread and central role of associative processes in generating goal-directed behavior, we believe they are likely the primary mechanism for spatial learning (Leising & Blaisdell, 2009). Associative processes are phylogenetically ancient, present in all animal phyla except Porifera (e.g., sponges), and underlie a wide range of learning phenomena, such as conditioned flavor preference and aversion, conditioned reflexes, sexual conditioning, timing, evaluative conditioning, and skill acquisition (Domjan, 2005). Blaisdell and colleagues, among others, have accumulated evidence that associative processes contribute to spatial learning across many foraging tasks, including the acquisition of spatial control by a landmark (Spetch, 1995), conditioned inhibition (Leising, Sawa, & Blaisdell, 2012), sensory preconditioning (Sawa, Leising, & Blaisdell, 2005), blocking (Leising, Wong, Ruprecht, & Blaisdell, 2014; see also Rodrigo, Chamizo, McLaren, & Mackintosh, 1997), overshadowing (Leising, Garlick, & Blaisdell, 2011; see also Chamizo, Rodrigo, & Mackintosh, 2006; Spetch, 1995), and occasion setting (Leising, Hall, Wolf, & Ruprecht, 2015). In these studies, punctate, visual landmarks served as spatial discriminative stimuli that signal the locations of a target instrumentally connected to a hidden food goal.

If spatial learning is governed by associative processes, then many important basic features of associative learning should be observable in spatial learning. Pavlov (1927) originally demonstrated that a classically conditioned response (CR) could be attenuated by presenting the conditioned stimulus (conditional stimulus [CS]) in the absence of the unconditioned stimulus (US). Pavlov found, however, that extinction learning tends to be transient, and is subject to spontaneous recovery over time (Pavlov, 1927, p. 58). This finding suggests that much of the original excitatory learning remained intact following extinction, and has been supported by more recent behavioral tests (e.g., Bouton, 1993; Hemmes, Brown, Jakubow, & Cabeza de Vaca, 1997; Pavlov, 1927; Rescorla, 1996). The transient (spontaneous recovery) or fragile (e.g., renewal, reinstatement, resurgence) nature of extinction learning indicates that once acquired, a CS–US association may be weakened, but cannot be erased. One type of control group used in a between-subjects design is a group (Control) that is tested immediately following extinction compared to a group tested following a longer retention interval (Spontaneous Recovery). Responding to the CS at test is greater in the Spontaneous Recov-

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ery Group than in the Control group. A second control consists of a within-subject design, with the subject receiving two separate CS–US pairings in Phase 1 of training, followed by extinction of both CSs. Subjects are then tested separately on one CS immediately following extinction and the other CS after a longer retention interval (e.g., Rescorla, 2004). Greater conditioned responding to the CS tested after the longer delay indicates spontaneous recovery. Though responding to the CS rarely recovers to preextinction levels even after long delays, the increase relative to short delays is evidence that the original CS–US association survived extinction.

In a series of experiments on the nature of extinction in a spatial task, Prados, Manteiga, and Sansa (2003) trained rats to search for a hidden platform in a Morris pool with four landmarks suspended above the edge of the pool. Following acquisition, the rats were placed in the pool with no platform (i.e., extinction) for eight consecutive trials. Test trials were conducted immediately following extinction (Group Delay-0) or 96 hr later (Group Delay-96, Experiment 3) with no platform. The amount of time spent in the platform quadrant indicated no preference for the platform quadrant during the last two trials of extinction and during testing for Group Delay-0. Group Delay-96 demonstrated extinction performance similar to that of Group Delay-0, but at test, Group Delay-96 spent significantly more time in the platform quadrant—thereby demonstrating spontaneous recovery. Spontaneous recovery has also been observed with mice in a Morris pool with a reversal procedure in place of extinction. Lattal, Mullen, and Abel (2003) trained mice to locate a hidden platform in one position of the pool, followed by a reversal training phase with the platform moved to the opposite side of the pool. The mice were then tested 1 day (1-Day) or 14 days (14-Day) after reversal training. Following the 14-day retention interval, mice spent more time searching for the platform in the initial training location compared with mice tested at 1 day. These between-subjects experiments demonstrate that spatial information regarding the location of hidden goal is retained during extinction.

Most conditioning paradigms measure the rate or magnitude of a response during acquisition, extinction, and during spontaneous recovery. However, a response can be characterized in many ways, including by its and temporal distributions. For example, Ohyama, Gibbon, Deich, and Balsam (1999, Experiment 3) trained pigeons in a Pavlovian key pecking procedure using an 8-s CS–US interval. By analyzing the temporal distribution of responses in addition to response magnitude, they found that presenting a CS in extinction significantly reduced the magnitude of the peak height, but the peak time of responding was maintained across sessions of extinction. Ohyama, et al. (1999) did not report tests for spontaneous recovery to determine how the temporal distribution might change following extinction.

We tested for extinction and spontaneous recovery of spatial control by a single landmark in a within-subject design. Each of four landmarks (A, B, C, and D) was presented on a touchscreen-equipped monitor and served as a spatial discriminative cue that signaled the location of a hidden target on the display. The target was located at a consistent distance and direction relative to each landmark. After acquisition, A and B were presented on separate nonreinforced extinction trials intermixed with reinforced trials of C and D to prevent any secondary extinction to C and D (e.g., Vurbic & Bouton, 2011). Nonreinforced test trials at different delays after extinction were then conducted. Extinguished LM A and nonextinguished C were tested two days following the last day of extinction (Immediate). We predicted that the extinguished A would elicit weaker spatial control relative to the target than would C. The Delay test was administered 14 days after the last day of extinction treatment, and consisted of extinguished B and nonextinguished D. If spontaneous recovery from extinction is observed, then spatial control (i.e., pecks to the target) by extinguished B should be better than by extinguished A (on the Immediate test). D served as a control for potential forgetting, and was expected to maintain high levels of responding to the target.

Method

Subjects

Six experimentally naïve White Carneaux pigeons (*Columba livia*) served as subjects. Subjects were individually housed in steel home cages with metal wire mesh floors in a vivarium. Experiments occurred at approximately the midpoint of the light portion of the 12-hr light–dark cycle. All subjects were under a food-restriction schedule and were maintained at 85% of free-feeding weight, but were allowed free-access to water and grit while in their home cages.

Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide × 36 cm deep × 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 × 30.5 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13 cm above the chamber floor. Pecks to the monitor were detected by an infrared touch screen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V house light located in the ceiling of the box was illuminated at all times, except when an incorrect choice was made. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the floor. All experimental events were controlled and recorded with a Pentium III-class computer (Dell, Austin, TX). A video card controlled the monitor in the SVGA graphics mode (800 × 600 pixels).

Procedure

Stimulus displays. A 20.3 cm wide × 17.8 cm high search space on the computer monitor was divided into an 8 × 7 grid. Each grid unit contained a 2-cm^2 response area that served as a possible target location, with 0.5-cm space between adjacent grid units. A 3-mm^2 dark-gray (RGB = 129, 129, 129) square marked the center of each cell of the 8 × 7 grid of response locations. This gray dot was not present when a square served as a landmark. Six visual stimuli served as landmarks. A pink “shield” and a purple “star” were used as training landmarks during pretraining and testing for all subjects. A blue “X” shape, an orange “U” shape, a green “R” shape, and a red “dumbbell” served as visual landmarks, which were counterbalanced across subjects. Each landmark image was 2 cm^2.

Pretraining. Subjects had previously been trained to retrieve mixed grain from the food hopper and had been autoshaped to peck a centrally presented white (RGB = 255, 255, 255) 2.5-cm circular ready signal. During each trial of pretraining, landmark T1 or T2 was presented and a reinforced target location was selected from the set of 56 possible grid locations. Landmarks T1 and T2 were presented at a fixed distance of 2.4 cm to the left or right of the target, respectively. Initially, the target location was visually marked with a 2-cm^2 gray (RGB = 224, 224, 224) square. The size (from 2-cm^2 to 3-mm^2) and brightness (from RBGs of 224 to 129) were altered within-sessions and between-sessions (depending on each pigeon's accuracy) until the target was indistinguishable from the gray squares at the other response locations (see Spetch & Mondloch, 1993). Initially, a single peck at the target caused the hopper to be illuminated and raised for 2.5 s. The response requirement was gradually increased over sessions, based on each bird's performance, from an FR-1 to a VR-3 schedule of reinforcement (range = 1 to 5). A trial ended without reinforcement and with a 30-s timeout with the house light extinguished if the pigeon met any of three conditions prior to reaching the requisite number of pecks at the target: three cumulative pecks at the landmark, 20 cumulative pecks at the set of nontarget locations, or failure to make any peck response for two consecutive minutes. Both correct and incorrect trials were followed by a 10-s intertrial interval (intertribal interval [ITI]) with the house light on. By the completion of pretraining, the target was marked with a 1-cm^2 medium-gray square for the first five trials of each 100 trial session. After the fifth trial, the target-marker was identical to those at all other grid locations (i.e., 3-mm^2 dark-gray square). Each session of 100 trials consisted of 50 trials each of T1 and T2 (which stimulus served as T1 or T2 was counterbalanced across birds).

Phase 1. Phase 1 treatment began after all subjects performed at or above 80% accuracy on two consecutive sessions with a VR3 reinforcement schedule. T1 and T2 were not presented again until testing. In Phase 1, pigeons received trials with four new landmarks during each 100-trial session. As in pretraining, the target location was visually marked with a 2-cm^2 gray (RGB = 224, 224, 224) square during the initial sessions of Phase 1 and gradually adjusted across sessions in congruence with the subject's performance. Landmark A, B, C, or D was pseudorandomly selected to be presented during a trial at a randomized location on the grid and with a consistent spatial relationship to the target. The location of each landmark to the target (North or South) was counterbalanced across birds, but with matching spatial arrangements for A and C and for B and D. Thus, for half of the subjects, the target was located 2.5 cm south of the center of landmarks A and C, and 2.5 cm north of the center of landmarks B and D. For the remaining subjects, the landmark-target relationships were reversed. On 23 trials with each landmark, pigeons were reinforced for meeting the response criterion. There were an additional two nonreinforced probe trials with each landmark that were 30 s in duration (ending without reinforcement) that served as probe trials to track performance during acquisition. Throughout Phase 1, a 30-s blackout (the house light and display turned off) was initiated for 20 cumulative responses to any location other than the target, three cumulative responses at the landmark itself, or 2 consecutive min with no responses. The blackout was followed by the next scheduled trial.

Phase 2. After reaching greater than 80% accuracy on two consecutive sessions during Phase 1 for each stimulus, Phase 2 began. In Phase 2, all trials with A and B consisted of 30-s presentations ending in no reinforcement (i.e., an extinction contingency was in effect). Each 100-trial session consisted of 25 nonreinforced presentations of A, 25 nonreinforced trials of B, and 25 trials each of C and D (23 reinforced and 2 nonreinforced for each landmark, as in Phase 1). Two criteria were used to determine when extinction was complete (a) mean responses to the target on trials with A and B during extinction dropped below 10% of the mean target responses on probe trials during the last three sessions of acquisition (Phase 1), and (b) the mean number of responses gathered on the first four of 25 trials with the extinguished landmarks (A and B) during extinction was similar to the mean from all of the extinction trials in a session.

Testing. Upon completion of Phase 2, and before the first set of tests, the subjects received a 60-trial retraining session with trials of only the training landmarks T1 and T2 in the same manner as during pretraining. Three test sessions followed retraining at each of two delay intervals following the last day of the extinction phase. The three test sessions of test Immediate were conducted beginning 48 hr after the last day of extinction treatment and consisted of nonreinforced probe trials with A and C. This 60-trial test session was composed of reinforced training landmark trials T1 and T2 for the first 20 trials, while the remaining 40 trials were composed of 32 reinforced trials of T1 and T2 (16 trials of each) and four nonreinforced trials each of A and C interspersed among the reinforced trials. The three test sessions of test delay were administered beginning 14 days following the completion of extinction treatment, and consisted of nonreinforced probe trials of B and D in the same manner as occurred for A and C in the Immediate test. On the test days, a trial with A, B, C, or D lasted for 30 s with no opportunity for reinforcement.

Measures and statistical analysis. Mean total pecks was calculated for each bird using pecks to all response locations (i.e., overall excitatory strength of the stimuli). Regarding spatial control, for each bird we calculated the percent pecks to each location by dividing the pecks at each location by the sum of pecks at all locations multiplied by 100. This measure differentiates between spatial control by a cue as a landmark or as a beacon (e.g., Mackintosh, 2002).

Effect sizes and confidence intervals for ANOVAs were computed using SPSS (IBM, New York) code (Smithson, 2001). Effect sizes and confidence intervals for post hoc tests were computed using the mean and standard deviations (Cohen, 1977). Some of our confidence intervals of the effect sizes suggest caution in their interpretation, as some of the analyses may be underpowered and fail to reveal underlying differences. Lastly, we include a Bayesian odds analysis for post hoc comparisons (see Gallistel, 2009) in which support for the null was critical.

Results and Discussion

Subjects received a mean of 32 Phase 1 sessions (*SD* = 4) to reach a criterion accuracy of >80%. There were no differences between landmarks during acquisition in mean total responses or mean target responses (Phase 1). A repeated-measures analysis of variance (ANOVA) conducted on the number of responses to the target location (target pecks) during the last four sessions of Phase

1 with Treatment (extinguished vs. nonextinguished) and Direction (above vs. below) as factors revealed no main effects nor the interaction $Fs(1, 5) \leq 2.83$, $ps > .05$.

The number of Phase 2 extinction sessions was determined by each subject's performance, with a mean of 13 sessions ($SD = 4$) to achieve both extinction criteria (see Supplemental Material). On the first day of extinction, the mean target pecks for all landmarks was 9.68 ($SD = 2.25$). By the sixth day of extinction (the last day for which all birds contributed data), mean target pecks had decreased for the extinguished landmarks ($M = .88$, $SD = .53$), but not for the nonextinguished landmarks ($M = 15.5$, $SD = 1.06$). This indicates that extinction affected responding to the target only on trials with the extinguished landmarks. An ANOVA conducted on the last session of Phase 2 confirmed a main effect of Treatment, $F(1, 5) = 203.19$, $p < .01$, $\eta_p^2 = .94$, 95% CI [.74, .99], but no main effect of Direction or interaction between factors.

A standard outlier analysis (two standard deviations above or below the mean) identified one subject who emitted little responding, to any location, at both test intervals. We excluded this subject's data from all subsequent analyses ($n = 5$). The total amount of responding (i.e., to any location) on trials of the extinguished landmark was not significantly greater during the delay ($M = 5.85$, $SD = 2.48$) than immediate ($M = 6.40$, $SD = 3.42$) tests across all three test sessions (see Figure 1, left panel). This observation was supported by a repeated-measures ANOVA conducted on total responses during the Immediate test with Session (1–3) and Treatment (extinguished vs. nonextinguished) as factors which revealed a main effect of Treatment, $F(1, 4) = 32.42$, $p < .01$, $\eta_p^2 = .89$, 95% CI [.26, .94], but no other main effects nor the interaction, $ps > .05$. The same analysis conducted on total responses during the Delay test again found a main effect of Treatment, $F(1, 4) = 20.32$, $p < .05$, $\eta_p^2 = .84$, 95% CI [.11, .91], and also a main effect of Sessions, $F(2, 8) = 6.76$, $p < .05$, $\eta_p^2 = .63$, 95% CI [.02, .78], but no interaction, $p > .05$.

Figure 1 (right panel) displays the percentage of target responses across six test sessions, consisting of three daily test sessions of A and C immediately (i.e., 2 days) following extinction, and three test sessions of B and D starting 14 days after extinction. A repeated-measures ANOVA conducted on the percentage of pecks to the target during the Immediate test with Session (1–3), and Treatment (extinguished vs. nonextinguished) as factors revealed a main effect of Treatment, $F(1, 4) = 52.44$, $p < .01$, $\eta_p^2 = .93$, 95% CI [.41, .96], and the interaction of Treatment by Session, $F(2, 8) = 4.59$, $p < .05$, $\eta_p^2 = .53$, 95% CI [.00, .72]. A similar analysis conducted on the percentage of pecks during the Delay test did not reveal any main effects, $Fs(1, 4) < 2.01$, $p > .05$ nor an interaction, $F(2, 8) = 1.34$, $p > .05$. Taken together, the main effect of treatment at the Immediate test, but not the Delay test, indicates spontaneous recovery of spatial control by the extinguished landmark at the Delay test, though not spontaneous recovery of the magnitude of instrumental responding (peck rate).

The data from Figure 1 indicate that responding became more variable across test sessions. Extinction was expected to occur during the four nonreinforced test trials of each session, and especially across all three test sessions. Variability in responding has been shown to increase during extinction. In particular, the standard deviation of pecks to a touchscreen has been demonstrated in pigeons to increase in the presence of stimuli associated with a low probability of reward (Stahlman, Roberts, & Blaisdell, 2010). Consequently, the following analyses are reported with data collected on Day 1 of testing at each test interval. A repeated-measures ANOVA performed on the percentage of target responses during the first session of each test with Treatment (extinguished vs. nonextinguished) and Test (immediate vs. delay) as factors revealed a main effect of Treatment, $F(1, 4) = 19.21$, $p < .05$, $\eta_p^2 = .83$, 95% CI [.09, .91], as well as an interaction, $F(1, 4) = 9.54$, $p < .05$, $\eta_p^2 = .70$, 95% CI [.00, .85]. Separate post hoc comparisons with a Bonferroni correction were conducted. Given these comparisons are critical to our conclusions, we also include results from a Bayesian odds analysis (see Gallistel, 2009). Post hoc tests revealed weaker spatial control by A than B ($p < .05$, $d = 1.25$, 95% CI [-12.69, 15.20]), and the odds against the null of 3.49 support its rejection; the results of both tests together indicate spon-

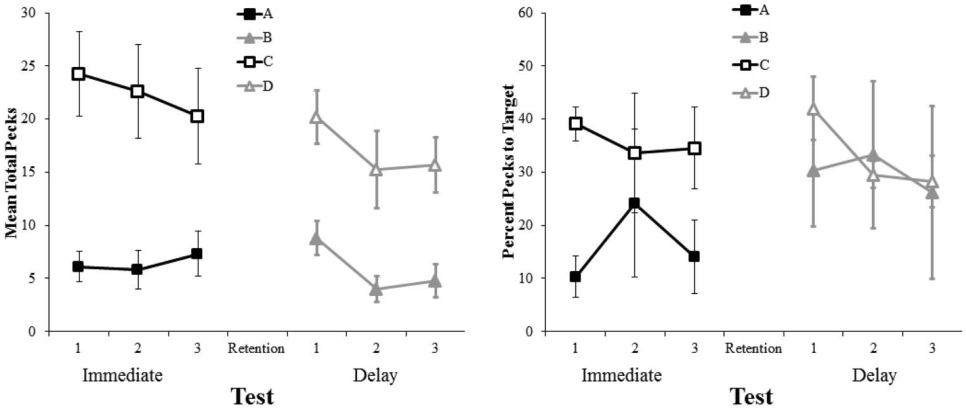

Figure 1. Mean total pecks and mean percent pecks to target across three test sessions at each delay. Total pecks were calculated for each bird as the sum of all responses to any location on the display, whereas, percent pecks was the number of response at the target divided by total pecks. Total pecks and percent pecks at the target are shown across 3 days of testing with landmarks A and C tested immediately (2 days) following Phase 2 and during delayed (14 days) tests of B and D. During Phase 2, pecks to C and D were reinforced but A and B were extinguished (nonreinforced). Error bars represent ±1 SEM.

taneous recovery from the immediate to the delayed test. The degree of spatial control did not differ between C and D ($p > .05$), and the odds in favor of the null of 1.70 weakly support the null hypothesis. Additional post hoc comparisons found weaker spatial control by the extinguished (LM A) than nonextinguished landmark (LM C) at the immediate test ($p < .05$, $d = 4.10$, 95% CI [−2.04, 10.25]), and the odds for rejecting the null of 88.77 strongly support rejecting the null. Spatial control at the delay test did not differ between extinguished (B) and nonextinguished (D) landmarks ($p > .05$), and the odds in favor of the null of 1.11 weakly support the null, suggesting a small but lasting effect of extinction treatment on spatial control. Additional tests conducted on the distribution of the response in the X and Y axes may further clarify whether spatial control recovered across the delay.

Figure 2 displays the percentage of pecks in the X and Y axes during the first test session with each landmark. Peak responding remains centered at the target during tests with each landmark. Nevertheless, the lower peak and broader distribution of pecks to LM A reveal loss of spatial control during the immediate test of an extinguished landmark. We used a chi-square test (cf. Leising et al., 2011; Sawa et al., 2005) to compare the distributions in each axis separately. The distribution of responses on nonextinguished landmark trials was selected as the expected data and the distribution on extinguished landmark trials as the observed. A chi-square test confirmed that the distributions from trials of the extinguished and nonextinguished landmarks during the immediate tests differed on both the X and Y axes, X^2s $(16) > 58.24$, $ps < .0001$. In contrast, the X and Y axes for the extinguished landmark at test delay were comparable to the nonextinguished landmark, X^2s $(16) < 16.55$, $ps > .41$. The accumulated evidence indicates that the percentage of responses at the target on delay tests with the extinguished landmark recovered to a level indistinguishable from that of the nonextinguished landmark. Consistent with what Ohyama et al. (1999) reported for extinction of temporal control of behavior, Figure 2 indicates that although the peak of target

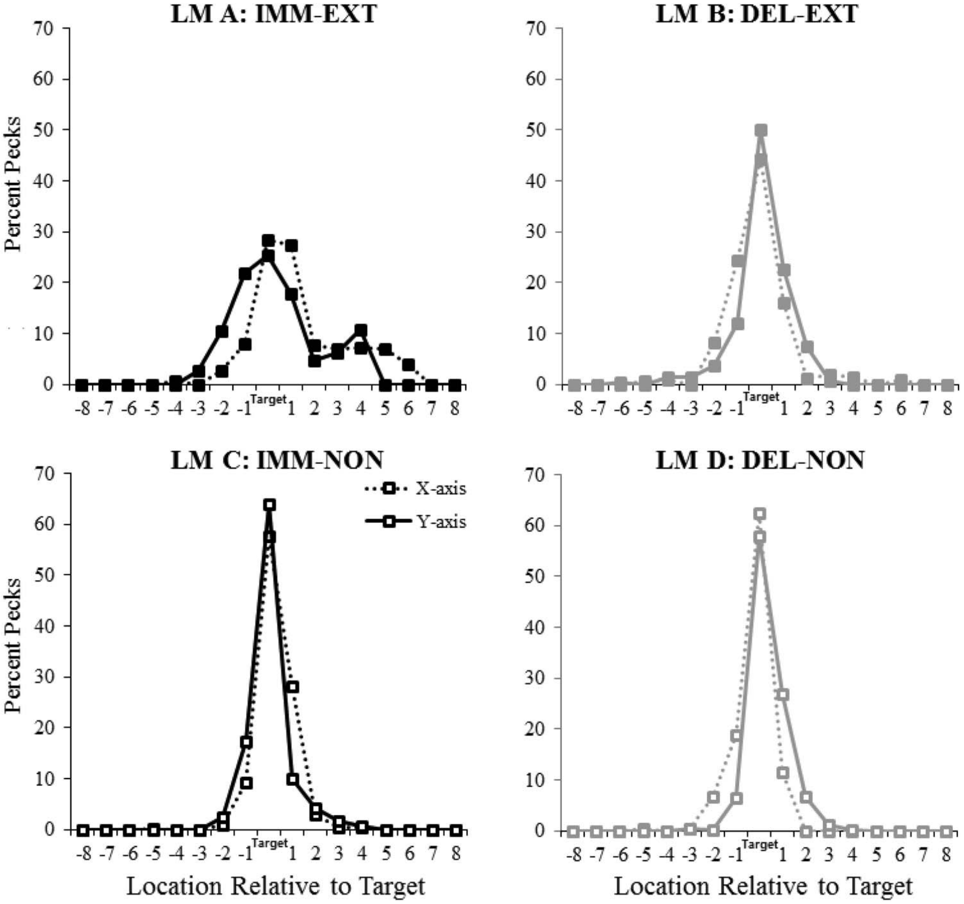

Figure 2. Distribution of percent pecks on the first test day with each landmark. Data from responses in the 8 × 7 grid of locations were standardized on each trial with respect to the position of the predicted target. The sign of values on the abscissa indicates pecks at grid locations to the left and right (− or +, respectively) of the target in the X axis or above and below (+ or −, respectively) the target in the Y axis. The absolute value of the point on the abscissa indicates the distance in the 8 × 7 grid of the peck from the target. During Phase 2, pecks to two landmarks were extinguished ("EXT"), whereas, pecks to the remaining two landmarks were reinforced ("NON"). Following Phase 2, the landmarks were tested immediately ("IMM") after Phase 2 or after a 14-day delay ("DEL").

pecks on trials with an extinguished landmark was reduced relative to a nonextinguished landmark, some amount of spatial control remained throughout extinction. We can conclude from these results that the originally trained spatial association between the extinguished landmark and the target location survived the extinction procedure, and remained latent until sufficient time had passed for spontaneous recovery of the association to occur.

Discussion

We developed a procedure to extinguish spatial control by a landmark and examined the degree of spontaneous recovery of an extinguished landmark following a short (2-day) or long (14-day) extinction-to-test interval. We found that while the total number of responses was low at both intervals for the extinguished landmark relative to the nonextinguished control landmarks—indicating a long-lasting extinction effect—the percent of target responses had recovered at the delay test, suggesting that spatial information conveyed by the extinguished landmark remained intact. In conventional learning paradigms, extinction constitutes new inhibitory learning, as opposed to memory erasure. We show the first evidence of spontaneous recovery in the spatial distribution of a response, which lends support to the assertion that extinction involves new learning that attenuates the originally acquired response.

Our results echo what has been reported regarding temporal control of responding in a key-pecking task (Ohyama et al., 1999) and spatial control of responding in the Morris water pool (Lattal, Mullen, & Abel, 2003; Prados et al., 2003). In our task, the dissociation between the rate or amount of pecking (for which no spontaneous recovery was observed) and the spatial control (which completely recovered) suggests a dissociation between perception (where, when, etc.) and decision confidence (how likely). This dissociation has also been observed in other learning paradigms (Balsam, Drew, & Yang, 2002; Gallistel & Gibbon, 2000; Gallistel, Mark, King, & Latham, 2001; Leising et al., 2015; Ruprecht et al., 2014). Said another way, it is as if following extinction the pigeons still knew where the target should be, given the presence of the landmark, but were not as confident as to whether the target would be there. A similar distinction has been made between whether a US will occur versus when it is expected to occur (Bouton, 1997). Thus, once acquired, spatial associations remain intact following procedures, such as extinction, that degrade performance. Nevertheless, the original spatial control can reemerge given appropriate circumstances, such as a delay or changes in the physical context.

Lattal et al. (2003) tested the renewal effect, which involves context manipulation to facilitate the reemergence of an extinguished response. All mice were trained to locate the position of hidden platform in the presence of four landmarks suspended above a pool in Context A, followed by a reversal learning phase in Context B with the same four landmarks but the platform relocated to the opposite side of the pool. Mice were then tested in either Context A or B with the platform removed. The mice tested in Context A showed a bias to search more often at the original platform location, whereas, rats tested in B spent more time searching at the opposite location. Spatial control by landmarks can survive extinction, as well as reversal learning (Prados et al., 2003).

Our result replicates the phenomenon of recovery of previously extinguished spatial control, and extends the phenomenon in a few important ways. First, instead of rodents, we used pigeons, an avian species that shares a most recent common ancestor with mammals approximately 275 million years ago. Second, our procedure involved an appetitive outcome, with an appetitive instrumental response (pecking), which contrasts with the instrumental escape response observed in a Morris pool. Third, we used a within-subject design such that each subject contributed to each type of test, immediate and delayed, with each type of cue, extinguished and nonextinguished. Finally, our procedure involved separate landmark-reinforcer associations, rather than an association between an array of landmarks and a location in space. Thus, our results demonstrate the generality of spontaneous recovery of spatial control.

Delamater (2012) has argued for a more comprehensive evaluation of extinction effects. Reports of partial recovery effects do not conclusively rule out an unlearning account such as that of Rescorla and Wagner (1972). Reports of the complete absence of recovery or of incomplete recovery, however, do lend support to an unlearning or masking account, respectively. In our task, recovery of spatial accuracy as measured by the distribution of percent pecks was nearly complete, which suggests little, if any unlearning occurred during extinction in our task, though we cannot rule out the possibility of some permanent extinction. Delamater (2012) also describes findings in which extinction has different effects on different aspects of learning (e.g., sensory, emotional, temporal, and hedonic). For example, Delamater (1996) trained rats in a Pavlovian-to-instrumental transfer test with two responses (lever press-pellets, chain pull-sucrose) and two CS–US pairs (tone-pellets, light-sucrose). One of the two CSs was then extinguished. Both CSs were then presented during the instrumental task. The sensory component of the extinguished CS–US association remained intact (selective transfer), whereas the response component (Pavlovian approach) was extinguished. Although we present evidence suggesting that the original landmark-target spatial association survives extinction, our data also suggest that the overall excitatory value of the landmark was weakened. This suggests the spatial and response components of the association may be affected differently by extinction, and is entirely consistent with Delamater's suggestion that extinction may have different effects on different components of learning. Nevertheless, it may be possible that under certain conditions both the response and sensory component may be unlearned or completely masked. This theoretical issue remains open to empirical scrutiny.

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