



Pigeons (*Columba livia*) Distinguish Between Absence of Events and Lack of Evidence in Contingency Learning

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When information about an event is perceptually occluded, individuals might recognize that the event may be present but that they cannot detect it because of the occluder. In such situations, an individual should continue to believe that the prevailing contingencies have not changed. This is in stark contrast to conditions where an expected event is explicitly absent, which should lead the individual to update their contingency knowledge. In an autoshaping procedure, we tested whether pigeons can discriminate conditions of perceptual ambiguity from perceptual certainty. Pigeons first learned to peck at two Pavlovian visual cues, followed by extinction of one of the cues. During extinction, the feeder was occluded by a metal shield for pigeons in Group Occluded, while the metal shield was placed next to but not covering the feeder for pigeons in Group Un-Occluded. On a final test with the metal shield removed, pigeons in Group Un-occluded pecked less at the extinguished cue than at the un-extinguished cue; while pigeons in Group Occluded pecked at an equally high rate to both cues. These results replicate in pigeons with similar results reported in rats by Waldmann et al. (2012) and show that pigeons are able to discriminate conditions of certainty from conditions of ambiguity.

Keywords: contingency, extinction, mental imagery, perceptual ambiguity, pigeons

Associative learning processes enable animals to learn predictive relations between events in the world and are ubiquitous throughout the animal kingdom. What makes an associative relation predictive is the contingency between the antecedent and subsequent event that stand in associative relation to each other. Thus, much of Pavlovian associative learning involves the detection of relations of contingency between events. Contingencies are not always stable and can often be nonstationary. That is, contingencies can change over time. Animals are not only sensitive to learning about contingencies but also learn when to update their knowledge after previously-learned contingencies have changed (Racy et al., 2011). Pavlov documented this through Pavlovian extinction learning (Pavlov, 1927). After initially learning an association between a light and food placed in the mouth, whereby the light would elicit a salivation conditional response, repeated presentations of the light in the absence of the food would lead to the extinction of the Pavlovian conditional response.

To successfully track and learn about changes in contingency, the animal must be able to detect that the contingency has changed. This is not always straightforward. Sometimes an event can be obscured from perceptual detection, such as by an occluding object or barrier, preventing its detection. That is, after learning a predictive relation between two events, A and B, such that A is predictive of B ($A \rightarrow B$), the absence of B in the presence of A could be due to two things. First, it could be due to a changed contingency, such as the case with Pavlovian extinction where the food no longer occurs following the presentation of A. Alternatively, however, the absence of B could result from an occluder preventing the individual from perceiving or accessing it even though it is actually still present. For example, a pigeon can learn that edible seeds can be found under a tree. As a result of this learning, the pigeon will spend time foraging under the tree. One day, the pigeon could arrive under the tree and not see any seeds. This could be due to the tree no longer producing those seeds (perhaps its fruiting season is over). It could also be due to the leaves of the tree having fallen off the branches and collected under the tree, thereby covering the seeds so that they cannot be seen by the pigeon. That is, the seeds are there but they are occluded by leaves. The pigeon would merely have to move the leaves out of the way to reveal the seeds to be eaten.

The above example makes it clear that in the real world, contingency detection is not always straightforward. The real world can be messy, and the messy nature of the real world can present the individual with perceptually ambiguous situations. This poses a dilemma: should the perceptual absence of an obscured event be automatically treated as its veridical absence, or should the individual suspend its belief that an event is actually absent if the perceptual situation is ambiguous? It seems logical that once a prior positive contingency has been strongly established, it should not be abandoned so easily. The process of reality monitoring should enable one to either adopt new learning about a changed contingency when it is unambiguous that contingencies have changed. In the example of the pigeon above, in the absence of leaves on the ground, the absence of seeds should indicate with certainty that the seeds are truly absent. On the other hand, the process of reality monitoring should also be sensitive to ambiguous situations, leading to slower learning about new contingencies when it can't be determined that they have changed. When leaves litter the ground, the pigeon should continue to believe that seeds might be present and that they are merely occluded by the leaves.

Updating contingencies in ambiguous situations should involve a process akin to reality monitoring. Reality monitoring involves the decision whether information initially had an external source or was derived from an internal source such as reasoning, imagination, or thought (Johnson & Raye, 1981). Like with reality monitoring, updating a belief about prevailing contingencies should reflect an ability to discriminate conditions of certainty that contingencies have changed from conditions of uncertainty that they have changed. Such a system should be designed to be less likely to update contingencies when there is less certainty that they have changed, that is when the individual has reasons to believe that they might not have changed.

We found that, like humans, rats can discriminate conditions where a change in prevailing contingencies has certainly changed from conditions where there is greater ambiguity that they have changed (Waldmann et al., 2012). Rats initially learned that light cues signaled the delivery of food into a food niche. Then, during an extinction phase, the light continued to be presented but in the absence of food. Feeder activity was measured as the interruption of an infrared photobeam projected across the opening to the niche. Thus, beam breaks served as a measure of the rat's expectancy of food given the light cue. For some rats, during extinction the food niche remained open as it had been during training, whereas for other rats, a metal shield was placed across the opening, thereby occluding access to the feeder. If rats had learned the initial light-food contingency, then detecting the unambiguous absence of food from an open feeder should have led to strong extinction learning whereby the contingency between the light and food should have been updated from a positive to a negative (or zero) contingency. Occluding the feeder, however, should have allowed rats to maintain the belief that the food might still be present, as it had been during the initial learning phase, but that it was inaccessible. That is, they might believe that the positive light-food contingency is still in effect and thus not extinguish the light-food association.

Waldmann et al. (2012) found evidence on a subsequent test with the occluder removed that rats in the occluded extinction condition continued to expect and look for food when the light was presented at test, whereas rats in the un-occluded extinction condition showed that they had learned to no longer expect food in the presence of the light.

In this study, we ask the comparative question of whether pigeons also understand that the absence of an event in perceptually ambiguous conditions does not necessarily reflect the true absence of the event. We used a similar procedure to that of Waldmann et al. (2012), where a visual cue is initially paired with a food outcome followed by a phase of extinction of the cue-outcome association and final testing of the cue. As in Waldmann et al. (2012) extinction was carried out with the food hopper either open (un-occluded) or occluded. Would pigeons, like rats, fail to show extinction of the cue-food association if extinction took place with the hopper occluded? Rather than food hopper entries as with rats, we used screen pecking behavior to assess the expectancy of food in the presence of the visual cue. We also used a mixed design, where each pigeon learned Pavlovian autoshaping to two separate visual cues, C and E (for “Control” and “Extinguished,” respectively), followed by extinction treatment of just Cue E and a subsequent test of both cues. If pigeons represent the food as still being delivered when the feeder is occluded during extinction, then at test they should show a similar level of autoshaped responses to both Cues C and E. Alternatively, pigeons that received extinction treatment with the feeder un-occluded should show lower rates of autoshaped screen response on test trials of Cue E than of Cue C.

Method

Subjects

Sixteen unsexed adult homing pigeons (*Columba livia*) from Double T Farms (Glenwood, Iowa) were used with $n = 8$ per condition (Covered and Uncovered). The pigeons had experience with an intelligence test battery but were naïve with respect to the current procedures and stimuli which were selected to minimize transfer from prior experience. Subjects were individually housed in steel home cages with metal wire mesh floors in a vivarium. They were maintained at 80% of their free-feeding weight, with free access to water and grit while in their home cages. Testing occurred during the light portion of the 12-hr light-dark cycle. Subjects were randomly assigned to one of two conditions ($ns = 2$): Occluded and Un-occluded. All procedures were approved by the UCLA Institutional Review Board.

Apparatus

The custom-built experimental apparatus consisted of five flat-black Plexiglas chambers (38 cm wide x 36 cm deep x 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M). The bottom edge of the viewing window was 13 cm above the chamber floor. Pecks to the monitor were detected by an infrared touchscreen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the chamber floor. The hopper was controlled by a micro-circuit motor (Pololu, Robotics and Electronics, Las Vegas, NV). The hopper could deliver 3-s access to mixed grain as a food reward from a hopper located behind a 4.5 cm square food aperture centered directly below the center touchscreen. The food hopper contained a mixture of leach grain pigeon pellets and seed (Leach Grain and Milling). All experimental events were controlled and recorded with personal computers running Windows 10 operating system. Stimuli were presented using the 2.7.11 version of Python with the Psychopy toolbox, version 3.0.3 (Peirce, 2007).

Stimuli

A blue (RGB = 0, 0, 255) and a yellow (RGB = 255, 255, 0) circle served as Cues C and E, counterbalanced within group. Each circle was 100 pixels (2.65 cm) in diameter.

Procedure

Phase 1: Autoshaping

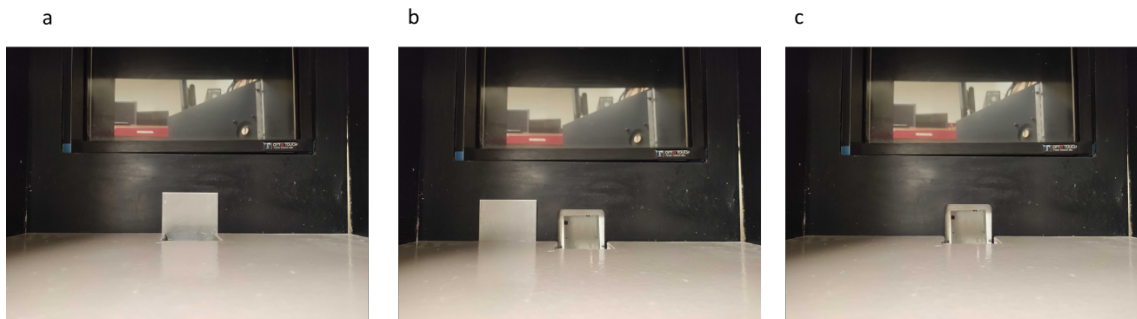
Pigeons had prior experience eating from the food hopper, and thus hopper training was not necessary. Pigeons received eight sessions, one per day, of training on an autoshaping procedure. Each session consisted of 40 trials, with Cue E presented on half of the trials and Cue C presented on the remaining trials. All parameters for trial number, trial length, and intertrial interval for autoshaping, extinction, and test procedures were selected based on prior unpublished data from our lab involving similar procedures. For half of the birds in each group, the blue circle served as Cue E and the yellow circle served as conditional stimulus (CS) C, with stimulus assignments reversed for the remaining birds in each group. On each trial, the cue was presented in the center of the black screen for 30 s and the hopper was raised for three seconds as soon as the Cue was removed from the screen at the end of the trial. The order of trials was randomized. An intertrial interval (ITI) of 30 s with a black screen separated trials. All screen pecks and all cue pecks were recorded during each trial. Any peck within 20 mm from the outer edge of the cue was counted as cue pecks.

Phase 2: Extinction

Pigeons received seven sessions, one per day, of extinction of Cue E. Cue C was not presented during this treatment phase. For Group Ocluded, the food hopper was covered by the metal plate attached with Velcro™ on the walls of the feeder thereby preventing visual and physical access to it (Figure 1a). For Group Un-occluded, the metal cover was placed against the wall of the enclosure, next to the opening to the food hopper, but without covering any part of the opening, thus leaving both visual and physical access to the hopper unimpaired (Figure 1b). Pigeons received 20 presentations of Cue E in each 30-min session, with a mean ITI of 35 +/- 5 s. Each 35-s presentation ended with the hopper being raised for 3 s. The hopper was empty of food, however, and thus none of the birds received food during these sessions.

Figure 1

A Photo of the Hopper Below the Touchscreen



Note. (a) When it was occluded by a metal shield during extinction, (b) un-occluded with the occluder next to the hopper during extinction, (c) when it was un-occluded with the occluder absent as during acquisition and testing.

In each phase, a discrimination index was calculated to assess expectancy of food during the cue. The discrimination index was calculated as the difference between the number of cue pecks during the 30-s prior to cue onset and the number of cue pecks during the 30-s cue presentation, divided by the sum of all cue pecks during the pre-cue and cue intervals. A discrimination index of zero indicates no difference in response rates pre and post cue onset, whereas a discrimination ratio greater than zero indicates a positive expectancy of food in the presence of the cue.

Phase 3: Test

The metal covers were removed from the operant chambers for both conditions (Figure 1c). All pigeons received a single 30-min extinction test session consisting of 10 presentations of each of Cue E and Cue C, in random order. None of these trials were reinforced, and the hopper was not raised on any of these trials. Trials without pecks were discarded from analysis. Because cue order was completely random, for each cue presented within the test session, we calculated the discrimination index for the first trial on which there was a response. For example, if Cue E was presented on Trial 1, it is possible for Cue C to be presented for the first time on Trial 2, or 3, etc. In all cases, both cues had been presented at least once by the 10th trial of the test session. The most stringent test of the hypothesis that occluding the feeder during extinction prevented extinction to Cue E is to analyze first trial performance for Cue E and for Cue C.

Results

Figure 2 presents the mean discrimination index (\pm 95% confidence intervals) for each Group (collapsed across Cues C and E given no cue differences, see below) as a function of session during the autoshaping acquisition phase. A mixed Analysis of Variance (ANOVA) conducted on the discrimination index with Group as a between-group factor, and Session and Cue as repeated measures, revealed a main effect of Session, $F(6, 90) = 5.52, p < .01$, but no effect of Group, $F(1,155) < 1.0$ or Cue, $F(1,15) = 1.61$, nor any interactions between factors. No other interactions were significant all $F_s < 1.0$. The increase in discrimination ratios across sessions shows that pigeons acquired the Pavlovian associations between both cues and food reward by the end of autoshaping acquisition.

Figure 2

Discrimination Index Mean and 95% Confidence Intervals for each Condition, Cue, and Session During the Autoshaping Acquisition Phase.

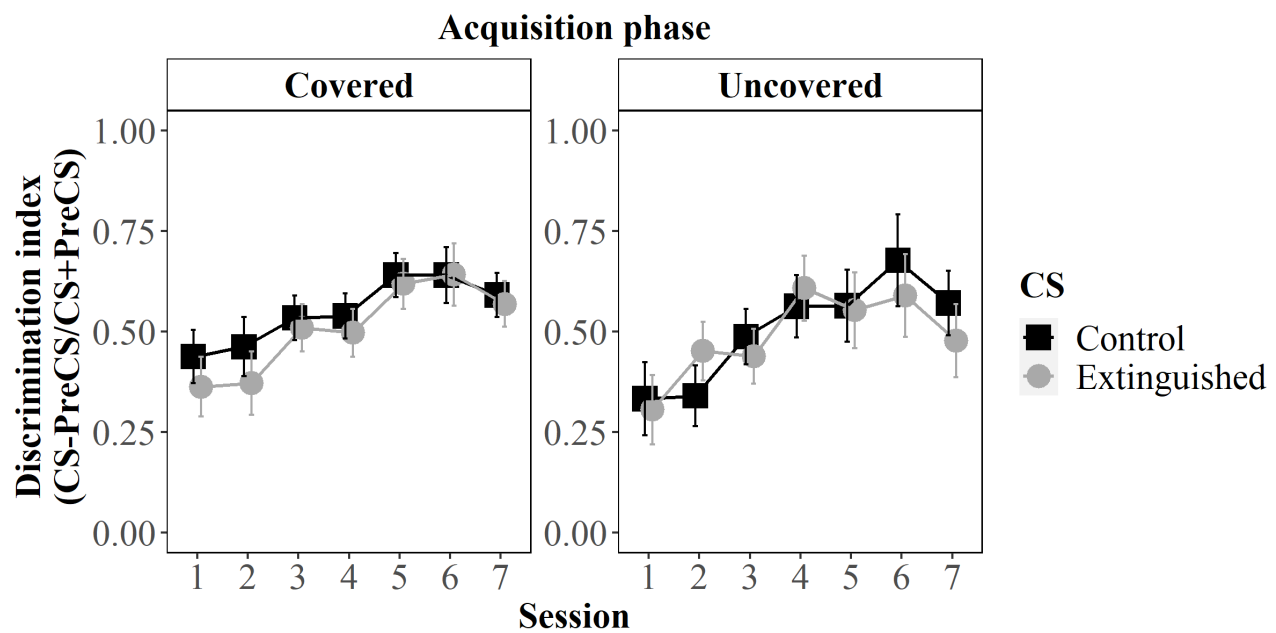


Figure 3 presents the discrimination index (\pm 95% confidence intervals) for each Group as a function of session during the extinction phase for Cue E. A mixed ANOVA conducted on discrimination index with Group as a between-group factor and Session as a repeated measure revealed an effect of Session, $F(6, 147) = 7.009, p < .001$, which indicates that all subjects had successfully extinguished pecks to Cue E by the end of extinction treatment. There was no effect of Group, $F(1, 147) = 1.40, p = .23$, nor a Group x Session interaction, $F(6, 147) < 1.0$.

Data from two subjects in Group Un-occluded were discarded due to no response during any Cue E trial of the test session. Data from an additional subject from Group Occluded was discarded for having a discrimination index for Cue E that was an outlier (-0.53). This resulted in a final n of nine subjects in Group Occluded and eight subjects in Group Un-occluded.

Figure 3

Discrimination Index Mean and 95% Confidence Intervals for each Condition and Session During the Extinction Phase to the Cue E

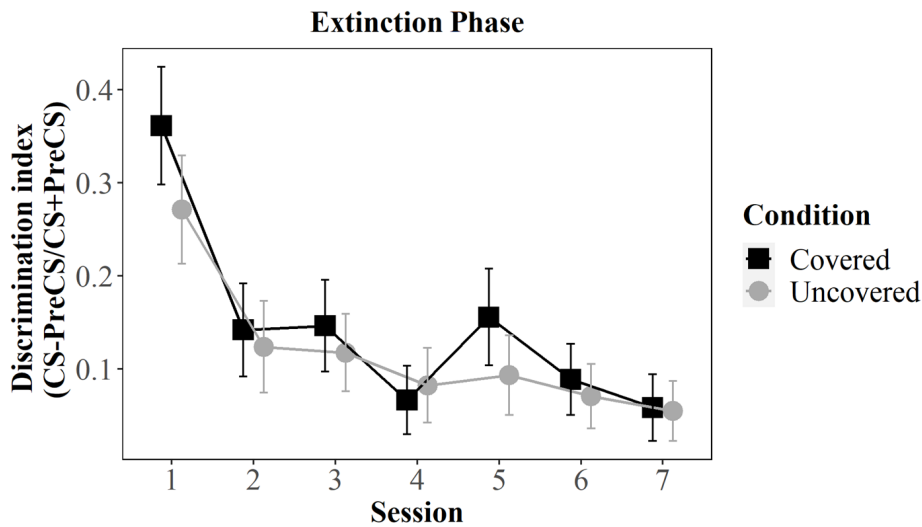
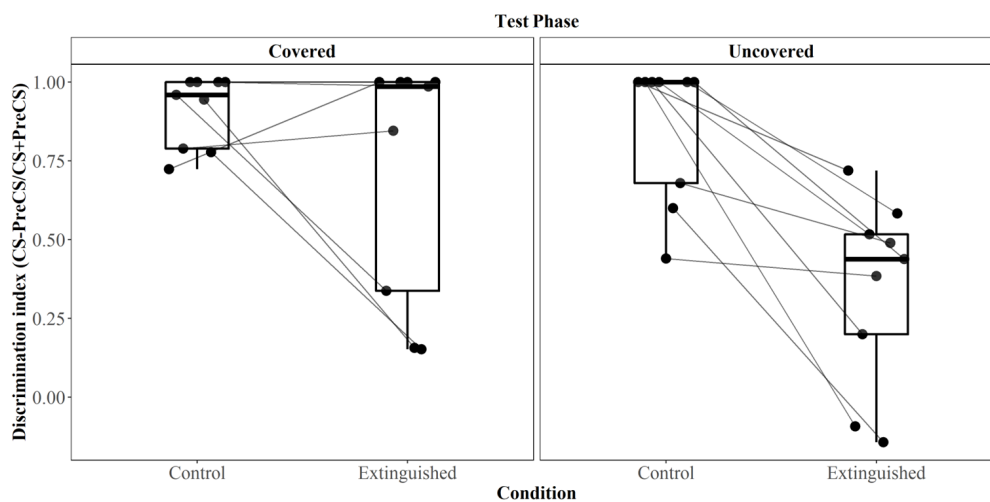


Figure 4 shows the mean discrimination index (+/- 95% confidence intervals) for each Group for the first trial with a response to Cue C and Cue E during the final test session. A QQ-plot analysis showed that the quantiles were skewed so a Shapiro-Wilk test was performed and showed that the distribution of the discrimination index departed significantly from normality ($W = 0.82, p\text{-value} < .01$). Thus, non-parametric analyses were used to analyze test results.

Figure 4

Boxplots Representing the Discrimination Index of each Subject of the First Response in each Cue During the Test Phase



Note. The whiskers represent the minimum and the maximum values, the black line is the sample median, and the boxes are the first and third quartiles. Lines connect data points for individual pigeons.

A Kruskal-Wallis test found an effect of group ($\chi^2(3) = 14.04, p = .002$). Post-hoc analysis was conducted using the Dunn test, which found higher responding to Cue C than to Cue E in Group Un-occluded ($p = .003$), thereby showing extinction to Cue E. No difference in responding to Cue C was found between Group Occluded and Un-occluded ($p = .47$), thereby showing that responding to the non-extinguished cue was not affected by extinction treatment in either group. More importantly, no difference in responding was found between Cue E and Cue C in Group Occluded, ($p = .22$), revealing that the drop in responding to Cue E during extinction by pigeons in Group Occluded was not due to extinction of the Cue E-Food association. Rather, the drop in responding during extinction was likely due to the reduced expectation of food while the feeder was occluded. As soon as the occluder was removed, pigeons in this group expected the food to be delivered on trials with Cue E.

This interpretation was also supported by the higher responding to Cue E in Group Occluded than in Group Un-occluded ($p = .01$), further supporting the protection from extinction of Cue E by occluding the feeder during extinction.

These results show that subjects that have the entrance to the feeder occluded did not show any extinction effect to Cue E compared to pigeons in Group Un-occluded for which the feeder was visually and physically available during extinction. The drop in responding during extinction for pigeons in Group Un-occluded likely reflected true extinction learning, as the pigeons continued to show low peck rates to Cue E during the test once the occluder that had been next to the feeder had been removed.

Discussion

We show for the first time that pigeons are able to discriminate conditions under which they should be certain to observe a contingency change from conditions where a change in contingency is ambiguous. After learning an autoshaped screen peck response to two visual cues, extinction of one of the cues resulted in a reduction in autoshaped screen pecks during extinction training. Nevertheless, if the feeder had been occluded during extinction, removal of the occluder at test resulted in an immediate increase in autoshaped screen pecks to the extinguished cue at a rate similar to a previously trained but non-extinguished cue. This result replicates in pigeons a similar result found in anticipatory goal approach behavior in rats (Waldmann et al., 2012).

As with the study by Waldmann et al. (2012), steps were taken to control for an alternative explanation of the increase in responding to Cue E at test in Group Occluded. This alternative is in terms of a renewal of responding to an extinguished cue. Bouton and King (1983) were the first to report that when cue extinction takes place in a different context (B) than where Pavlovian conditioning was first established (A), that conditioned responding renews when tested in the original Context A.

One could make the argument that an ABA type of renewal effect could explain the results in Group Occluded in our study. That is, if the introduction of the metal shield during extinction constitutes a contextual change, then the drop in responding observed during extinction might remain specific to the extinction context, that is, the context with the shield present. Removal of the shield at testing might be considered a change back to the original training context, and thus, a renewal of cue-elicited screen pecks. It was to control for this alternative that we explicitly added the metal shield to the operant chamber during extinction for Group Un-occluded. The only difference was that, for Group Un-occluded, the shield was placed next to the food hopper, while in Group Occluded it was placed over the hopper, thereby preventing birds from accessing the feeder. The metal shield was removed from the operant chamber for pigeons in both groups, thereby creating a context change back to the conditions of original acquisition for pigeons in both groups. The fact that responding to Cue E increased at test only for pigeons in Group Occluded, but not for pigeons in Group Un-occluded, argues against a renewal interpretation of our results.

An additional difference between our study and that of Waldmann et al. (2012) was the nature of the response measure. In the experiments by Waldmann et al. (2012), food expectancy was measured as entries into the food niche. This behavior was prevented during extinction, thereby preventing them from measuring extinction online (i.e., while it was happening). In our current study, however, food expectancy was measured by screen pecks to the visual cues presented on the screen. These were not prevented by the occluder, and thus, we were able to monitor extinction behavior while it was happening. Furthermore, the removal of the occluder from over the feeder did not change the nature of the visual cues presented on the screen, and thus any change in cue response from extinction to test could not be due to any artifact of the occluding procedure *per se*. Rather, it must be explained by the change in how the pigeons perceived and treated the meaning of the cue during the two phases.

These results add to the growing list of phenomena shown in our laboratory demonstrating that rats, and now pigeons, understand that conditions of stimulus ambiguity are discriminable from conditions of perceptual certainty. This has been shown both when the food outcome has been made ambiguous as in this study and that of Waldmann et al. (2012), as well as, for rats, conditions of cue ambiguity (e.g., Blaisdell et al., 2009; Fast & Blaisdell, 2011; Fast, Biederman, et al., 2016; Fast, Flesher, et al., 2016; see review by Blaisdell, 2019). The question remains whether pigeons will also show an ability to discriminate situations of cue ambiguity from unambiguous situations.

The ability to discriminate conditions of ambiguity from unambiguous situations would seem to require a process akin to reality monitoring – where one can tell whether one should be able to detect an event or whether an event should be difficult or impossible to detect given prevailing conditions, such as the presence of an occluder. We have argued that this ability reflects the operation of a process of mental imagery. Are pigeons capable of mental imagery? While some have discounted this possibility based on empirical data (e.g., Hollard & Delius, 1982), others have reported positive evidence for visual mental imagery in pigeons (Neiwirth & Rilling, 1987). Our current results are more consistent with evidence that pigeons do have some capacity to mentally represent a stimulus in its absence.

The investigation of how animals learn about the absence of an event has received relatively little attention among invertebrate phyla. Abramson and colleagues have studied avoidance learning in various invertebrates (e.g., bees, crabs, and earthworms; Abramson, 1986; Abramson et al., 1988; Abramson & Buckbee, 1995). These studies show that it is not the absence of an event (a punishing stimulus) that is reinforcing but the fact that the punishing stimulus is paired with the instrumental avoidance response. Another study from the same laboratory investigated proboscis extension response (PER) conditioning in bees using two CS, both paired with a US (Abramson et al., 2013). In one condition, the CS was the addition of an odor; in the second, the CS was the turning off of an odor. The bees responded to the presentation of the CS but not to its absence (analogous to a feature-positive/feature-negative effect). Thus, the evidence that currently exists suggests that invertebrate phyla do not directly learn about the absence of an event. This contrasts with vertebrates which do learn about absent events. Further research on learning about absent events in invertebrates is needed to determine whether a true difference exists between vertebrates and all other animal phyla.

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