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Imagine That! Cue-Evoked Representations Guide Rat Behavior During Ambiguous Situations

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Mental imagery involves the perceptual-like experience of an event that is not physically present, or detected by the senses. Fast and Blaisdell (2011) reported that rats use the representation of an associatively retrieved event to guide behavior in ambiguous situations. Rats were reinforced for lever-pressing during 1 of 2 lights but not both lights. They were then tested with 1 light illuminated while the second light was either covered by an opaque shield (ambiguous) or uncovered and unlit (explicitly absent). Rats lever-pressed less when the second light was covered compared with unlit, suggesting that a representation of the ambiguously absent light guided their behavior. However, Dwyer and Burgess (2011) offered an alternative mechanism in which the explicit absence of a cue gains associative value during training. Covering the light at test could effectively remove these associative properties, resulting in a generalization decrement of behavior. The current experiments were designed to test contrasting predictions made by these 2 accounts. Experiment 1 empirically established that generalization decrement can occur when an element of a compound cue is presented alone at test, but this decrement is attenuated, rather than enhanced, when the absent element is covered. Experiment 2 utilized a conditioned inhibition procedure to demonstrate that rat behavior during cue ambiguity is driven by an associatively retrieved representation rather than by generalization decrement. Collectively, the results argue against a purely nonrepresentational associative account of behavior and support a role for associatively retrieved representations in rats.

Keywords: imagery, ambiguity, configural, rat, representation

Einstein claimed, "Imagination is more important than knowledge. For knowledge is limited" (Einstein & Shaw, 1931/2009, p. 97). No doubt imagination plays a crucial role in the lives of humans. Enabling consideration of events without direct experience through the senses, imagination contributes to flexible and innovative approaches to novel situations and may be adaptive in changing environments. It is likely that the ability to imagine evolved from evolutionarily precursory processes, such as the ability to retrieve a memory or representation. These precursory mechanisms could bridge the gap between knowledge attained through experience and imagining novel possibilities by allowing the memory of a perceptually absent event to influence behavior. In this paper, we ask the question: Are rats able to retrieve a representation of a perceptually absent event, and does this retrieved representation (or image) participate in behavioral decisions?

Contemporary research on representation-mediated conditioning procedures (e.g., Pickens & Holland, 2004) demonstrates that an associatively retrieved image can substitute for its physical occurrence to drive learning in humans and rats alike. For example, rats that experienced a tone-flavor combination later developed an aversion for the flavor when only the tone was paired with injection of LiCl. These rats consumed less flavored food than rats that had not experienced the tone paired with LiCl or rats that had not learned the tone-flavor association before the tone was paired with LiCl. Holland (1981) argued that the tone-flavor pairings allowed the tone to retrieve a representation of the flavor. The retrieved flavor representation was sufficient to establish a flavor aversion to the food, despite the food having never been directly paired with the illness. In fact, learning occurs to the retrieved image (e.g., flavor) even when behavior does not change to the physically present mediating cue (e.g., the tone; cf., Holland, 1981, 1983, 2006). Nonetheless, imagination (as Einstein popularly used the term) involves more than accumulation of additional knowledge, but the ability to use imagery to make predictions in the face of uncertainty. Work in our lab suggests rats possess this representational capacity. That is, rats may use an associatively retrieved image to guide behavior when a relevant stimulus is blocked from physical detection (Blaisdell et al., 2009; Fast & Blaisdell, 2011; Waldmann et al., 2012).

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Fast and Blaisdell (2011) trained rats on an instrumental discrimination with two lights (A and B) serving in either a positive patterning (A−, B−, and AB+; where the '+' and '−' refer to the presence and absence of food reinforcement, respectively) or negative patterning (A+, B+, and AB−) discrimination. Rats were then tested with only A lit while B remained unlit (explicitly absent) or occluded from view with an opaque shield (ambiguous whether B is lit or unlit). An interesting find was that only negative patterning rats responded differently when B was covered compared with when B was unlit. However, in a second experiment, rats tested on a positive patterning discrimination were found to respond differently when light B was covered compared with unlit if the rats had also learned negative patterning with auditory cues. An important find was that if B had served in positive patterning, rats responded more when it was covered compared with unlit; however, if B had served in negative patterning, rats responded less during test trials with A lit while B was covered compared with unlit. This pattern is consistent with the rat behaving as if it were guided by an image of the physically covered light B; responses during AB training trials were always reinforced for positive patterning but never for negative patterning. We refer to this use of an image as the Representational Account.

While we interpreted these results as evidence that rats can use an associatively retrieved representation to guide their behavior when a relevant stimulus is blocked from detection, Dwyer and Burgess (2011) offered an alternative explanation, which we will term the Nonrepresentational Account. Although they do not dismiss the possibility that rats may retrieve representations of absent events, Dwyer and Burgess (2011) argue that this process is not necessary for rats to behave differently in our test conditions. Instead, they suggest the solution strategy of negative patterning involves learning that both the illumination and nonillumination of a light can serve as cues to predict the outcome. In other words, negative patterning requires learning a configuration of lit and unlit bulbs during training (see also Rescorla, 1972). Moreover, this form of configural learning could transfer to how rats learned about lit and unlit bulbs serving in the positive patterning discrimination (Alvarado & Rudy, 1992; Williams & Braker, 1999, 2002). Thus, expectancy of reinforcement during a trial with only one bulb lit is driven by both the illumination of that bulb and the explicit nonillumination of the other bulb. Negative patterning involving lights A and B is typically represented as A+, B+, and AB−; however, by Dwyer and Burgess' (2011) account, the same discrimination could be represented as $A_{ON}B_{OFF}+$, $B_{ON}A_{OFF}+$, $A_{ON}B_{ON}-$, where "ON" and "OFF" refer to the lit and unlit bulb in the conditioning context. Given this associative structure, A_{ON} alone is insufficient to predict reinforcement because it is also present during nonreinforced trials when it occurs with B_{ON}. Although B_{OFF} alone is unlikely to develop a strong excitatory association (because it is also present during the nonreinforced intertrial interval) B_{OFF} is actually more predictive of reinforcement when it occurs with A_{ON} than A_{ON} itself. Dwyer and Burgess (2011) argue that covering B's bulb during test trials with A_{ON} effectively removes B_{OFF}, and its corresponding excitatory association with the reinforcer. This produces a reduction (relative to A_{ON} with B_{OFF}) in the expectancy of reinforcement and, likewise, a reduction in lever pressing. While both the Representational and Nonrepresentational Accounts can explain our results (Fast & Blaisdell, 2011), they use very different mechanisms. The Nonrepresentational Account involves the removal of relevant associative values, akin to generalization decrement (Ghirlanda & Enquist, 2003). That is, the rat's behavior on any trial consists purely of responses elicited by the present cues. More important, this explanation does not require the rat to distinguish between tests with B covered or unlit, instead the rat is predicted to behave differently when relevant cues with nonzero associations to the reward are missing. On the other hand, the Representational Account asserts that the behavior of the rat is determined not only by associations to the reward from the present cues, but also associations to the reward from representations of absent cues. As demonstrated by representation-mediated conditioning experiments, the representation of an absent cue is retrieved by the present cues to which it is associated. More important, a cue's representation should be retrieved by its associate regardless of whether the cue is explicitly present (e.g., B_{ON}) or absent (e.g., B_{OFF}). When the cue is present, the representation remains active; however, the explicit absence of the cue may weaken influence of the associatively retrieved representation on behavior. When the presence or absence cannot be confirmed (such as when the cue is covered by an opaque shield), the associatively retrieved representation of the cue remains active to direct responding, even in the cue's physical absence. Without implying that the rat perceives this ambiguity, the Representational Account explains how a rat distinguishes between a cue that is explicitly absent versus concealed by using a retrieved representation of the concealed cue to guide behavior.

The present experiments investigate if rat behavior when a relevant cue is ambiguous is driven by a retrieved representation of the hidden cue, the Representational Account, or generalization decrement, the Nonrepresentational Account. In Experiment 1, rats learned to approach a feeder for sucrose in the presence of an AB compound consisting of a click (A) and light (B; Figure 1, left panel). Rats were then tested with presentations of the AB compound or A alone. A-Alone tests were conducted with B either unlit (Figure 1, top right) or covered by an opaque shield (Figure 1, bottom right). According to both theoretical accounts, more feeder approaches were expected on AB than on A-alone tests when B was unlit, because of generalization decrement. If the cover allows the rat to maintain a representation of B, we should expect a high rate of feeder approach on A-alone test trials with B covered. Such a result would show that processes of generalization decrement exert different behavioral control when a cue is rendered ambiguous. It would not, however, distinguish the Representational and Nonrepresentational accounts. Experiment 2 specifically examines these possibilities, using a Pavlovian conditioned inhibition training procedure.

Experiment 1

Materials and Method

Subjects. Twenty female Long-Evans rats (*Rattus norvegicus*) acquired from Harlan (Indianapolis, IN) served as subjects. Subjects were approximately 120 days old at the start of the experiment. They had a previous experimental history in our laboratory with tones and lever pressing for sucrose solution in a different set of conditioning chambers than those used in this study, but naïve with respect to the stimuli serving in this study. Subjects were pair-housed in transparent

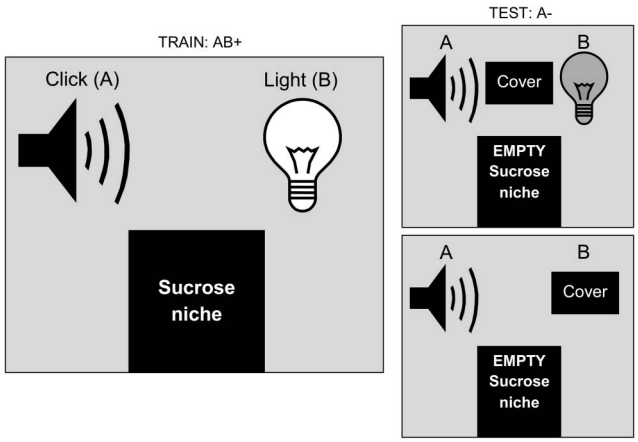

Figure 1. Left panel: Schematic of training treatment for Experiment 1. A click (A) and a light (B) were presented simultaneously for 10 s followed by delivery of sucrose unconditioned stimulus (US) in the niche. Top Right panel: Schematic for test treatment of A alone with B uncovered and unlit. A metal shield was placed to the left of B. Bottom Right panel: Schematic for test treatment of A alone with a metal shield placed directly over B, thereby covering B. In addition to each of these types of test trials, rats also received tests of AB with the shield located to the left of B. No sucrose was delivered on test trials. '+' represents sucrose delivery, '−' represents no sucrose delivery.

plastic tubs with a wood shaving substrate in a vivarium maintained on a reverse 12-hr light/dark cycle. Experiments were conducted during the dark portion of the cycle. A progressive food restriction schedule maintained rats at 85% of their initial free-feeding weights. The procedures used in this and the following experiment were conducted under approval and following the guidelines established by the IACUC of UCLA.

Apparatus. Four experimental chambers, measuring 30 × 25 × 20 cm (L × W × H) were housed in separate sound- and light-attenuating chests (ENV-008, Med Associates, Georgia, VT). The front and back walls and ceiling of the chambers were constructed of clear Plexiglas, the side walls were made of aluminum, and the floors were constructed of stainless steel rods measuring 0.5 cm in diameter, spaced 1.5 cm center-to-center.

Each chamber was equipped with a water-dipper (ENV-202M, Med Associates) that could be lowered into a trough of 20% sucrose solution and raised. When in the raised position, a small well (0.05 ml) at the end of the dipper arm containing sucrose solution protruded up into the drinking niche. The opening of the drinking niche was equipped with an infrared beam and photodetector to record entries into the drinking niche. A speaker on the ceiling of the chamber delivered a click train (4/s) 5 dB(A) above background (62-dB produced by a ventilation fan and white noise generator) to serve as cue A. A diffuse 28 V light (ENV-227M, Med Associates) was located on the right-side chamber wall, 6 cm from the ceiling and 4 cm from the front wall. This light was flashed in a pattern of 0.4 s on alternated with 0.1 s off to serve as cue B. Otherwise, the chamber remained normally dark. A 4-cm square solid stainless steel cover, designed to mimic a covered light bulb, could be affixed to the metal wall of the chamber.

Procedure.

Magazine training. Rats were trained to drink from the dipper containing sucrose solution by lowering and raising the dipper every 20 ± 15 s (actual intertrial interval [ITI] values = 5, 10, 15, 20, 25, 30, and 35 s) in a 60-min session.

Conditioning. Our conditioning procedure was adapted from Bouton, Doyle-Burr, and Vurbic (2012). In the first 38 min session, all rats received eight 10 s presentations each of A and AB (2 min variable ITI) to habituate any unconditional orienting behaviors. On each of the next four 76-min sessions, rats received 32 AB-sucrose pairings. Each 10-s presentation of compound cue AB was preceded by a 10 s precue period, and was followed immediately upon termination with delivery of sucrose solution. The dipper remained in a raised position throughout the ITI, allowing access to its contents until the next scheduled sucrose delivery.

Testing. Rats received two 11-min test sessions, with one additional day of Conditioning intervening between the tests. No sucrose was presented during test sessions and a variable 2-min ITI separated trials. In Test Session Cover, B's light was replaced with the stainless steel cover and rats received four 10-s trials of A alone. Test Session Uncovered was similar to Covered with the exception that the cover was placed next to B's light and rats received two trials of AB and two of A alone. Test trials during the Uncovered test session were delivered in one of two orderings: 1 (A, AB, AB, and A) or 2 (AB, A, A, and AB), counterbalanced across rats. The order of test session, Covered or Uncovered, was counterbalanced across subjects.

Data analysis. Conditioned responding was assessed with elevation scores computed by subtracting the number of nose poke responses during the 10-s preconditional stimulus (CS) period from the number of nose pokes during the CS. Elevation scores for each subject were calculated for each trial and then averaged across trials within subject. We next calculated the difference between mean elevation scores during Testing for each test condition. Lastly, we utilized Gallistel's (2009) software (http://cognitivegenetic.rutgers.edu/ptn/) to compute a Bayesian odds analysis for post hoc comparisons in which support for the null was critical. A large Bayesian odds value is evidence in support of the null hypothesis that the two comparison samples are drawn from the same population, whereas a small value provides support against the null hypothesis.

Results and Discussion

At the end of conditioning, subjects demonstrated that they had learned the AB-sucrose association with a mean elevation score of 33.92 (SD = 17.50). An outlier analysis performed on elevation scores at the end of acquisition identified one subject with a score that was more than 2 SDs below the mean. The test data from this subject were therefore removed from further analysis. Elevation scores remained high (M = 28.86, SD = 15.20) during the conditioning session intervening between the two test sessions, indicating that the first day of testing did not disrupt conditional control of nose poking by stimulus AB.

A repeated-measures analysis of variance (ANOVA) conducted on elevation scores during testing found no main effects of Test Order, nor did Test Order interact with any other factors, all Fs < 1.0. Likewise, a repeated-measures ANOVA conducted on amount of nose poking during the pre-CS period found no differences between test conditions, F < 1.0; thus, showing that all tests started from a similar baseline (AB: M = 10.05, SD = 18.65; A: M = 16.34, SD = 21.29; A with B Covered: M = 9.57, SD =

8.22). Additional pairwise Bayes tests of the Null hypothesis found a Bayes Factor of 11.91 for AB versus A, and 28.19 for AB versus A with B Covered, thereby providing evidence for the Null hypothesis that the pre-CS responses did not differ. Figure 2 shows mean elevation scores during each test trial type. A repeated-measures ANOVA revealed a main effect of Test Trial Type, $F(2, 36) = 3.67$, $p < .05$, $\eta_p^2 = .17$. Planned comparisons revealed that the mean elevation score on AB test trials was higher than on A alone test trials, $F(1, 18) = 4.69$, $p < .05$, indicating a decrement in generalization from AB to A alone. This replicates the generalization decrement effect reported by Bouton et al. (2012) that our procedure closely matched. The important test of our hypothesis comes from the test of A alone but with B's light bulb covered. On this Covered test trial, the mean elevation score was very similar to that on AB test trials, $F < 1.0$, and a Bayes factor of 17.71 supports the null hypothesis that these two tests sample the same populations of responses. Responding on the Covered test was marginally greater than on A-alone test trials, $F(1, 18) = 4.11$, $p = .058$ and a Bayes factor of 1.43 supports rejecting the Null hypothesis that these two tests sample the same population of responses. Additionally, single-sample t tests comparing mean elevation scores on each type of test revealed that both the AB and Covered tests were significantly above zero, $t(19) = 3.61$, $p < .01$ and $t(19) = 4.93$, $p < .001$, respectively, while A was not different from zero, $t < 1.0$. Thus, the presence of the cover over Light B's bulb prevented generalization decrement despite only cue A being presented.

Comparison across test conditions was performed by calculating difference scores between each pairwise comparison (Cumming, 2014). The estimated difference between AB and A alone was 14.69, 95% confidence interval (CI) [1.39, 27.99]. The estimated difference between A alone compared with A with B Covered was 10.44, 95% CI [.034, 20.54]. The estimated difference between AB and A while B was Covered was 4.25, 95% CI [−4.67, 13.17]. We calculated standardized Effect Sizes (ES) using Cohen's d (Cohen, 1988), with the pooled SDs across the conditions being compared. The ES of generalization decrement in responding to A alone was large, $d = 0.74$. The ES for abolishing generalization decrement by covering B's light bulb at test was moderate, $d = 0.65$. The ES for the difference between A while B was Covered and AB test conditions was $d = 0.27$. Thus, by covering B, we were able to prevent generalization decrement from AB when testing with A alone.

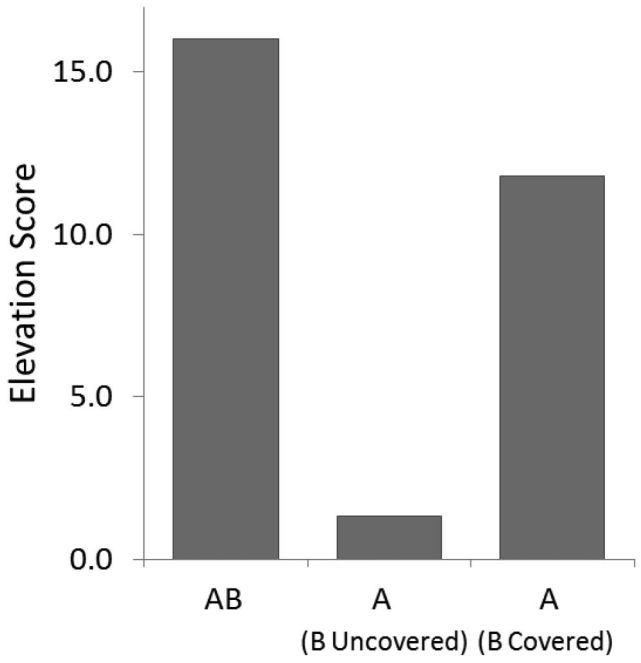

Figure 2. Mean elevation scores (nose pokes during CS—nose pokes during the pre-CS period) for each test condition during the test phase. AB indicates tests with compound CS AB. A (B Uncovered) indicates tests with A alone and B's bulb uncovered. A (B Covered) indicates tests with A alone and B's bulb covered.

Experiment 2

While Experiment 1 demonstrated that covering an absent cue (B) with an opaque shield prevented generalization decrement, it remained unclear if this effect was driven by removing inhibitory associations between the unlit bulb (B_{OFF}) and food (Nonrepresentational Account), or by the retrieval of a representation of the absent (covered) light B (Representational Account; Figure 3). During A-alone test trials with B unlit, the excitatory cue B_{ON} is either explicitly absent or cue B_{OFF} is present. B_{OFF} was expected to inhibit responding because it never occurred with food during training. Therefore, according to the Nonrepresentational Account, removing B_{OFF} (by covering the bulb) should invigorate responding. According to the Representational Account, the occurrence of A should retrieve a representation of B_{ON}. This representation (and its excitatory association with the outcome) should be maintained when B is Covered, thereby invigorating behavior. Thus, despite using different mechanisms, both accounts accurately predict the increased behavior demonstrated during A-alone test trials with B Covered. Experiment 2 distinguishes between the Nonrepresentational and Representational Accounts using a Pavlovian conditioned inhibition design (see Figure 4).

Rats learned to anticipate sucrose delivery whenever they heard an auditory cue (A), unless it occurred while a light (X) was simultaneously lit (A+, AX−). If unlit cues acquire signal value, this procedure should cause X_{ON} to predict the absence of food whereas the unlit bulb (X_{OFF}) would predict food delivery when it occurs in the presence of A_{ON}. Rats also learned that another auditory cue (B) was always followed by sucrose and never occurred with X. Probe trials of A or B were conducted while X (the putative inhibitor) either was unlit or covered. The Nonrepresentational Account predicts that removal of (covering) X's unlit bulb should equivalently decrease anticipatory behavior to each cue (A and B). In other words, the excitatory associative value of X_{OFF} would be missing from both A-alone and B-alone trials when X was covered. Conversely, because only A had occurred in the presence of X during training, the Representational Account predicts that only A should cause rats to retrieve a representation of X when X is covered. This prediction is based on the observation that representation retrieval relies on within-compound associations between presented cues and retrieved representations (Castro, Wasserman, & Matute, 2009; Dickinson & Burke, 1996; Liljeholm & Balleine, 2009). Thus, A should be uniquely poised to activate the representation of inhibitor X, which should, in turn, reduce

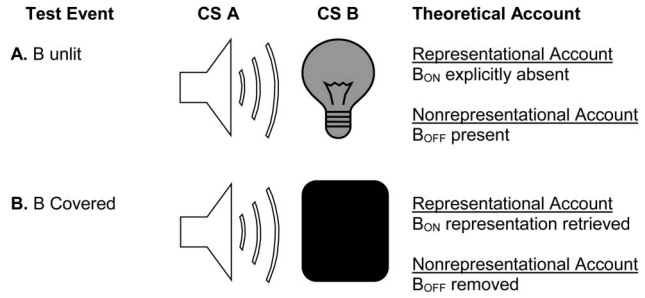

Figure 3. Schematic representation of proposed mechanisms mediating behavior when a relevant cue is blocked from detection. (A) During A-alone test trials with B unlit, the excitatory B_{ON} is either explicitly absent, or the inhibitory cue B_{OFF} is present. (B) When B is covered at test, the Representational Account proposes that A retrieves a representation of light B. This representation (and its related associations with the outcome) influences behavior. If B predicts that the outcome will occur, behavior will be invigorated (Experiment 1); however, if B predicts that the outcome will not occur, behavior will be suppressed (Experiment 2) relative to when B's absence is explicit (Panel A). Alternatively, the Nonrepresentational Account suggests that covering light B removes cue B_{OFF}, leaving only the A_{ON} association to drive behavior.

sucrose expectancy. Thus, the Representational Account predicted reduced responses to A when X was covered compared with unlit, but no change in behavior to transfer excitor B, regardless of the status of X (unlit or covered). This result would show that rats utilize retrieved representations to direct behavior when relevant cues are occluded from perception. While the critical test of these contrasting accounts involves the summation tests, we followed up with retardation-of-acquisition tests to fully document conditioned inhibition with our procedure.

Materials and Method

Subjects. Twenty-two experimentally naïve female Long-Evans rats approximately 90 days old at the start of the experiment were acquired from Harlan (Indianapolis, IN). Subjects were housed and maintained as in Experiment 1. Rats were randomly assigned to either Group Covered or Uncovered (*n*s = 11).

Apparatus. All aspects of the apparatus were as described for Experiment 1, with the exception that the incandescent bulb with a plastic diffuse shield (ENV-227M, Med Associates) located on the right-side chamber wall, was flashed at a rate of 2 Hz to serve as the conditioned inhibitor, X (or Y, counterbalanced). An additional 28-V house light (ENV-215M, Med Associates) directed toward the ceiling was located on the right-side chamber wall, 6 cm from the ceiling and 4 cm from the rear wall to serve as Y (or X, counterbalanced). In addition to the ceiling speaker capable of emitting a click-train, one speaker located on the left wall of the chamber could deliver a high-frequency tone (3,000 Hz) 8 dB(A) above background. The tone and click train served as A and B, respectively.

Procedure. All sessions terminated after 60 min (unless otherwise noted).

Magazine training. One single session, identical to the procedure described in Experiment 1, trained rats to approach and drink from the dipper.

Magazine training with stimulus pre-exposure. To reduce the novelty of all cues (cf., Bouton et al., 2012) each stimulus (A, B, X, and Y) was presented twice randomly for 30 s with a mean ITI of 415 s (ITI values = 370, 400, 430, and 460 s). Otherwise, this session was identical to magazine training.

Conditioned inhibition training. During this and all subsequent phases of the experiment, stimuli were presented for 30-s and were separated by a mean ITI of 160 s (range:120–200 s). Trials were quasi-randomly presented with the restriction that no more than two of the same type could occur consecutively. During each training session, rats received 6 A+, 6 B+, and 6 AX− trials. A+ and B+ trials involved presentation of the auditory cue immediately followed by delivery of the sucrose solution unconditional stimulus (US). No US was delivered following AX− presentations. In this manner, A and B were trained as excitatory Pavlovian CSs to predict the US whereas X was trained as a conditioned inhibitor to predict the absence of the US.

Cumulative duration of nose pokes into the food niche were recorded during a 30 s period before CS onset, during the 30 s CS presentation, and during a 10 s period after CS termination. This enabled us to calculate elevation scores as our measure of conditional responding (CR) by subtracting the duration of nose poking during baseline from nose poking during the CS. Subjects were required to demonstrate mastery of the conditioned inhibition discrimination by committing substantially more CRs to A+ and B+ trials compared with AX− trials during three out of five

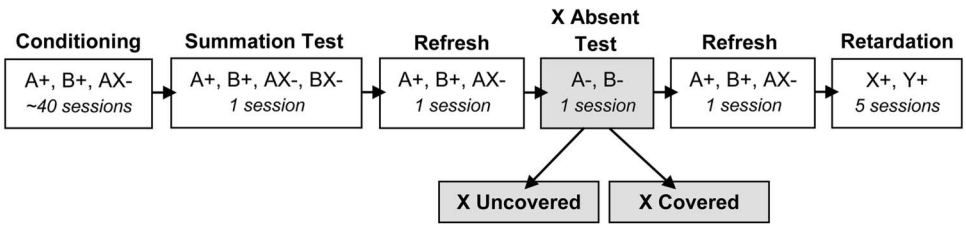

Figure 4. Experiment 2 design. Subjects required approximately 40 sessions to master the conditioned inhibition training. After demonstrating mastery of the discrimination, subjects received a summation test in which the ability of X to inhibit responses to another well-established CS (B) was assessed. Following summation, one refresh session identical to conditioning was conducted. Rats then received the critical X absent test in which probe trials of A and B were presented while X was explicitly absent (Uncovered) or ambiguous (Covered). Subjects then received one additional refresh session before advancing to the retardation-of-acquisition test of inhibition.

consecutive sessions and during the two most recent sessions. Because sessions only occurred 6 days a week, subjects never advanced to test sessions after a day off, but instead received one additional day of conditioned inhibition training. If the subject again met criterion, it advanced to testing during the subsequent session.

Summation test. In this single 40-min test session, subjects experienced 3 A+, 3 B+, and 3 AX− trials identical to the preceding conditioned inhibition training. Additionally, 3 BX− trials served to measure X's ability to transfer inhibitory influence over CRs otherwise elicited by B (Rescorla, 1971). This test is conventionally used to demonstrate that subjects recognize the elements constituting the compound AX− trials from training, rather than perceiving the compound as a unique, third, cue. This distinction is important to our experimental question regarding physically absent cues or elements.

Conditioned inhibition refresher session. To ensure that the standard summation test had not disrupted previously acquired CRs, one additional session of conditioned inhibition training was conducted on the day after the summation test. All subjects met test criteria during this session.

X absent test. During this single 20-min session, subjects received 3 A− and 3 B− trials. For subjects randomly assigned to the Covered condition, these trials occurred with X covered (the light bulb on which X had been presented in training was replaced by solid stainless steel cover). Subjects assigned to the Uncovered condition received the same A− and B− probe trials but with X's light bulb remaining in place and uncovered. As in Experiment 1, we positioned the cover centrally above the food niche and immediately adjacent to X for subjects in the Uncovered condition. More important, X remained unlit during this session for all subjects.

Conditioned inhibition refresher session. After the X absent test, 10 subjects were removed from the experiment to serve in an unrelated manipulation. This left 12 subjects (six subjects from each test group) to complete this session and the following retardation-of-acquisition sessions. These subjects received a minimum of one conditioned inhibition training session to ensure that the X absent test had not disrupted previously acquired CRs. Subjects were again required to demonstrate successful discrimination before advancing to the retardation-of-acquisition test.

Retardation-of-acquisition test. In conjunction with the Summation Test, this phase allowed us to assess inhibitory learning (Rescorla, 1971). During these sessions, the putative inhibitor (X) was trained with an excitatory contingency. If prior training truly established X as an inhibitor to predict the absence of the US, significantly more training should be needed for subjects to learn this new, contradicting excitatory association compared with the amount of training needed to establish an excitatory association to a different neutral stimulus (Y). Additionally, this test rules out a distraction explanation for successful summation results, hence the necessity for both tests in assessing conditioned inhibition (Rescorla, 1971). The 12 subjects that completed the preceding conditioned inhibition refresher session received 9 X+ and 9 Y+ trials. This test continued for five sessions. Response rates were compared between X and Y within and across training sessions to serve as an index of learning rate (Rescorla, 1971). One subject from the Uncovered group was removed from the experiment because of health concerns after completing four of the five sessions of retardation.

Results and Discussion

All subjects behaved according to the Pavlovian conditioned inhibition contingencies (Figure 5A) in an average of 40 training sessions (M = 40.46, 95% CI [32.86, 48.05]). A mixed ANOVA on nose poke elevation scores (CRs) from the final session of conditioned inhibition training across the three trial types (A+, B+, and AX−) and between the two assigned test conditions (to-be-Covered and to-be-Uncovered) failed to reveal any effects or interactions with assigned test condition, ps $> .2$, indicating that both conditions demonstrated equivalent levels of conditioned inhibition performance at the conclusion of training. Because no group differences were found, a repeated-measures ANOVA collapsed across assigned test conditions was computed on CRs from the final session of conditioned inhibition across the three training trial types. The main effect of Trial Type ($F(2, 42) = 49.18$, $p < .01$, $\eta_p^2 = .70$), was further analyzed with planned comparisons between the training trial types. Reflecting appropriate discrimination between the training contingencies, subjects responded at equally high levels to A and B (Bayes Factor = 4.17), but demonstrated significantly fewer CRs to AX− trials compared with A-alone trials, $F(1, 21) = 46.21$, $p < .001$, $\eta_p^2 = .69$, with an estimated difference between the means of 744.95, 95% CI [517.05, 972.86].

Summation Test CRs were analyzed with a mixed ANOVA across the four trial types (A+, AX−, B+, and BX−) and between the two assigned test conditions (to-be-Covered or to-be-Uncovered), revealing no effects of test condition, ps $> .09$. Thus, a repeated-measures ANOVA collapsed across the assigned test conditions was computed across the four standard summation trial types (Figure 5B). A main effect of Trial Type $F(3, 63) = 24.08$, $p < .001$, $\eta_p^2 = .54$, was further analyzed with planned comparisons to reveal that CRs did not differ to A and B, $F(1, 21) = 1.35$, $p > .20$, Bayes Factor = 4.24, as found at the conclusion of conditioned inhibition training. Also consistent with training performance, CRs to AX− were significantly less than A, $F(1, 21) = 34.93$, $p < .001$, $\eta_p^2 = .63$, with an estimated difference between the means of 319.82, 95% CI [207.28, 432.35]. More important, all subjects passed the summation test by responding significantly less to the novel BX trials compared with B-alone, $F(1, 21) = 19.64$, $p < .001$, $\eta_p^2 = .48$, with an estimated difference between the means of 248.72, 95% CI [132.00, 365.45].

The most critical results to our hypothesis involve performance during the X absent test (see Figure 6). A mixed ANOVA computed on CRs with test stimulus (A and B) as the repeated-measure and test condition (Covered and Uncovered) as a between-subjects factor revealed a significant Stimulus X Condition interaction, $F(1, 20) = 8.10$, $p = .01$, $\eta_p^2 = .29$. No other effects were significant, ps $> .2$. Planned comparisons revealed that subjects experiencing A while the inhibitor, X, was Covered, responded significantly less than subjects tested on A with X Uncovered, $F(1, 20) = 8.63$, $p = .008$, $\eta_p^2 = .30$, with an estimated difference between the means of 169.82, 95% CI [49.27, 290.37]. However, there was no difference in responses to B, regardless of whether X was Covered or Uncovered, $F < 1.0$, Bayes Factor = 3.56. Furthermore, rats responded significantly less to A while X was Covered at test

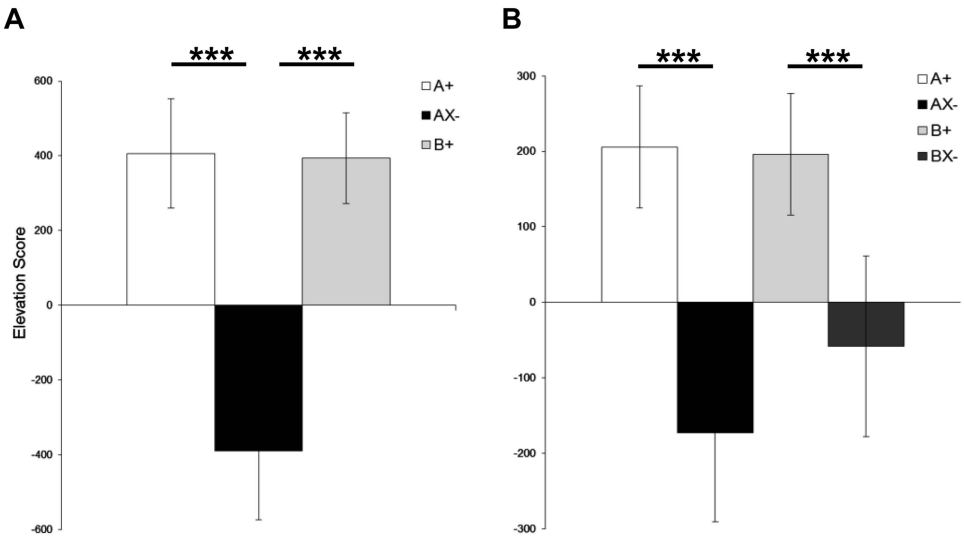

Figure 5. Experiment 2 mean elevation scores (nose poke duration during CS—nose poke duration before CS). Error bars represent the 95% confidence interval, '***' reflect differences between compared trials (indicated by the horizontal line positioned over the bars) at the .001 level of significance. At the conclusion of training (A), subjects responded at equivalently high levels to both CS A (white bars) and CS B (gray bars) with a significant reduction during AX− trials (black bars). Subjects maintained high levels of CRs to both CS A (white bar) and CS B (light gray bar) and reduced responding to AX− trials (black bars) during the summation test (B) while also showing reduced CRs to novel BX trials (dark gray, rightmost bar) compared with B trials, as evidence of successful summation.

compared with A-alone trials occurring during the preceding summation test (when X was explicitly absent), $F(1, 10) = 7.92$, $p = .018$, $\eta_p^2 = .44$ with an estimated difference between the means of 91.55, 95% CI [19.06, 164.03], but did not show any differences in responses to B during the same sessions, $p > .70$, Bayes Factor = 3.21 or when X was Uncovered ($ps > .30$, Bayes Factors = 2.59 and 2.51 for A-alone and B-alone trial types, respectively).

Although rats tested with X Covered demonstrated negligibly lower baseline responses ($M = 94.36$, 95% CI [9.01, 179.71]) than rats tested with X Uncovered ($M = 118.64$, 95% CI [33.29, 203.99]), this difference was not significant, $F(1, 20) = 0.18$, $p = .68$, $\eta_p^2 = .009$, Bayes Factor = 2.75, and fails to explain our test results. Because our test dependent measure subtracted baselines, this slight difference between the conditions would be expected to artificially inflate test responses for the Covered condition relative to Uncovered. Our test results reveal the opposite: Covered responded less during A-alone probes than Uncovered. Furthermore, baselines did not differ within-subjects between A and B trials ($M = 56.36$, 95% CI [21.48, 91.25]) when X was covered, $F(1, 10) = 1.62$, $p = .23$, $\eta_p^2 = .14$, Bayes Factor = 2.12, indicating that the reduced responding to A but not B during this test was also not an artifact of baseline differences.

Retardation-of-acquisition results were analyzed using a mixed ANOVA with session and trial type as within-subject factors and previous test condition as a between-subjects factor. This revealed a Session X Group interaction, $F(4, 36) = 4.57$, $p = .004$, $\eta_p^2 = 0.34$ and a Trial Type X Group interaction, $F(1, 9) = 15.43$, $p = .003$, $\eta_p^2 = 0.63$. Planned comparisons revealed that although subjects did not initially treat X and Y differently, $t(11) = 1.41$, $p = .19$, $d = 0.41$, Bayes Factor = 2.30, responses to Y significantly increased by the third, $t(11) = -2.85$, $p = .016$, $d = -0.90$ and fifth, $t(10) = -3.85$, $p = .003$, $d = -1.40$ session of retardation, but did not change to X at any point across the five sessions ($ps > .07$, Bayes Factors = 4.05, 3.81, 2.39, 1.83 across the five sessions, respectively, Figure 7A). Collectively, these results suggest retarded acquisition of an excitatory association with the putative inhibitor X, compared with the control CS Y.

Subsequent comparisons were performed to investigate the surprising Group interactions and determine if the cover position during the X absent test influenced how subjects performed during retardation (Figure 7B). Subjects tested on A and B while X was Covered did not initially treat X and Y differently, $t(5) = -0.53$, $p = .62$ (Bayes Factor = 2.45), however, they showed a trend to increase CRs to Y by the fifth retardation session, $t(5) = -2.44$, $p = .058$, $d = 2.19$ ($ps > .30$ for all other sessions) while not changing how they responded to X during the equivalent period of the retardation test, ($ps > .58$, Bayes Factors = 2.18, 2.89, 2.10, and 2.32 across the five sessions, respectively). Furthermore, despite treating X and Y identically during the first retardation session, these subjects tended to treat the two cues differently by the fifth session, $t(5) = -2.25$, $p = .074$, $d = 2.01$, by evincing more CRs to Y than X. The same was not true for subjects that experienced X Uncovered during the X absent tests of A and B. These subjects showed a significant increase in CRs to X by the third session of retardation, $t(5) = -5.53$, $p = .003$, $d = 2.38$, that was maintained through the fourth, $t(5) = 7.64$, $p = .001$, $d = 3.22$ and fifth sessions, $t(4) = -3.38$, $p = .028$, $d = 1.60$. Thus, only subjects experiencing X Covered during the X Absent Test showed signs of retarded acquisition of an excitatory association to X, despite the two test conditions demonstrating equivalent conditioned inhibition training and summation performances.

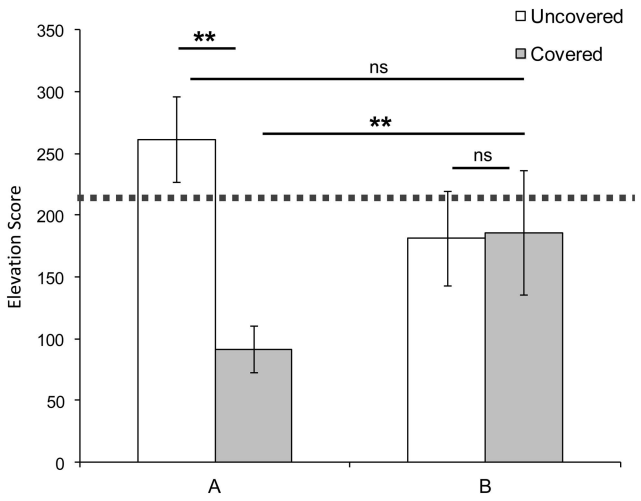

Figure 6. Mean elevation scores (nose poke duration during CS—nose poke duration before CS) during the critical X absent test. Error bars represent the 95% confidence interval, '**' reflect differences between compared trials (indicated by the horizontal line positioned over the bars) at the .01 level of significance while 'ns' indicates nonsignificant differences. The horizontal, dashed line represents mean CRs to CS A and CS B (that did not differ) during the preceding standard summation session. Responses to B (right) did not differ, however, subjects responded significantly less to A (left) when X was Covered (gray bars) compared with Uncovered and unlit (white bars).

This surprising group difference in retardation was explored with a mixed ANOVA examining A+ responses during the refresh training session that proceeded, and the session that followed the X absent test as a repeated-measure, and test condition as a between-subjects factor. This revealed a Session X Condition interaction, $F(1, 20) = 12.93$, $p = .002$, $\eta_p^2 = 0.39$, that was assessed with t test comparisons. Although pretesting responses did not differ between the test conditions, $t(20) = -1.26$, $p = .22$, $d = -0.56$, Bayes Factor = 3.54, subjects tested on A and B with X Uncovered responded significantly less during the first A+ refresh trial after the test than during the first A+ trial that preceded the test, $t(10) = 4.15$, $p = .002$, $d = 2.63$ (Figure 7C), with an estimated difference between the means of 76.27, 95% CI [35.34, 117.21]. Responses to A+ trials pre- and posttest did not differ for rats tested with X Covered, $t(10) = -0.59$, $p = .57$, $d = 0.37$, Bayes Factor = 2.91. We address possible theoretical implications for the reduced responding to A following tests with X Uncovered and potential influence on subsequent retardation-of-acquisition performance in the General Discussion.

General Discussion

The results of Experiment 1 demonstrate generalization decrement in Pavlovian feeder approach when rats were tested on one auditory element (A alone) from a previously trained audio-visual compound (AB). Generalization decrement was attenuated, however, by covering the visual element (B) at test. This result is consistent with the results of prior research from our lab (Blaisdell et al., 2009; Fast & Blaisdell, 2011), examining the difference in responding to a cue that is explicitly absent versus obscured by an opaque cover at test. One possible explanation for our results is that presentations of A elicited a representation or expectation of B, because A and B were perfectly correlated during training. When B's bulb is uncovered and B is off, the absence of B is explicit. Thus, the rat recognizes that the test situation is different from that of training; its observations do not match its expectations. When B's bulb is covered by an opaque shield, however, B's status is ambiguous and the retrieved representation of B remains active to influence behavior.

An alternative Nonrepresentational Account offered by Dwyer and Burgess (2011), explains the attenuation of generalization decrement during Covered test sessions by assigning signal value to the unilluminated bulb as a cue (B_{OFF}). During training, B_{OFF} is consistently paired with a lack of food during the ITI, allowing it to acquire inhibitory value. Thus, when A is presented at test, B_{OFF} suppresses conditioned feeder approach. However, covering B's bulb at test removes this inhibitory B_{OFF} cue to effectively increase feeder approach during Covered versus Uncovered test sessions. Dwyer and Burgess (2011) utilized the ALTSim program (Thorwart, Schultheis, Konig, & Lachnit, 2009) to simulate the results of Fast and Blaisdell (2011) using 'ON′ and 'OFF' cue representations. Indeed, ALTSim accurately simulates Experiment 1 performance when stimulus representations of A_{ON}, A_{OFF}, B_{ON}, and B_{OFF} (with default α values) are applied to Pearce's (1994) configural model (Figure 8A). Note, while inclusion of ITIs in the simulation failed to influence the overall pattern of predicted test performance, the simulation only accounts for our test results with inclusion of Cue_{OFF} representations because these are removed when the cue is covered at test as the only means to distinguish between uncovered and covered test conditions.

Nonetheless, even with the Cue_{OFF} representations, the simulation fails to predict our results from Experiment 2 (Figure 8B) because it predicts equivalent reduction in responding to both A and B when X was covered at test. In Experiment 2, rats successfully learned a Pavlovian conditioned inhibition procedure, evincing fewer CRs to A when it occurred with X compared with when it occurred independently. More important, X inhibited CRs to another well-established CS (B) during a summation test and elicited fewer CRs compared with a previously neutral cue (Y) after five sessions of excitatory training (Rescorla, 1971). Collectively, these results indicate that X had successfully acquired inhibitory value during training. Not surprisingly, rats tested with X uncovered and unlit (explicitly absent) during the X absent test demonstrated CRs similar to A and B trials from training. Of greater interest is the behavior during A and B probe trials while X was covered (ambiguously absent). According to the Nonrepresentational Account, and our ALTSim simulation of Pearce's (1994) model, CRs should be equally reduced to A and B while X was covered because both trials involved removal of the unlit bulb (X_{OFF}) that had acquired excitatory value. Alternatively, our Representational Account predicted that only A would retrieve a representation of the inhibitory X during the ambiguous test, because only A had been paired with X during training to establish an A-X association. Once retrieved, this representation of X could exert behavioral control by reducing the expectancy of the US. Thus, we predicted fewer CRs to A compared with B when X was covered. The results supported our Representational Account, rats made significantly fewer CRs to A compared with B when X was covered, and showed a summation effect with fewer CRs to A

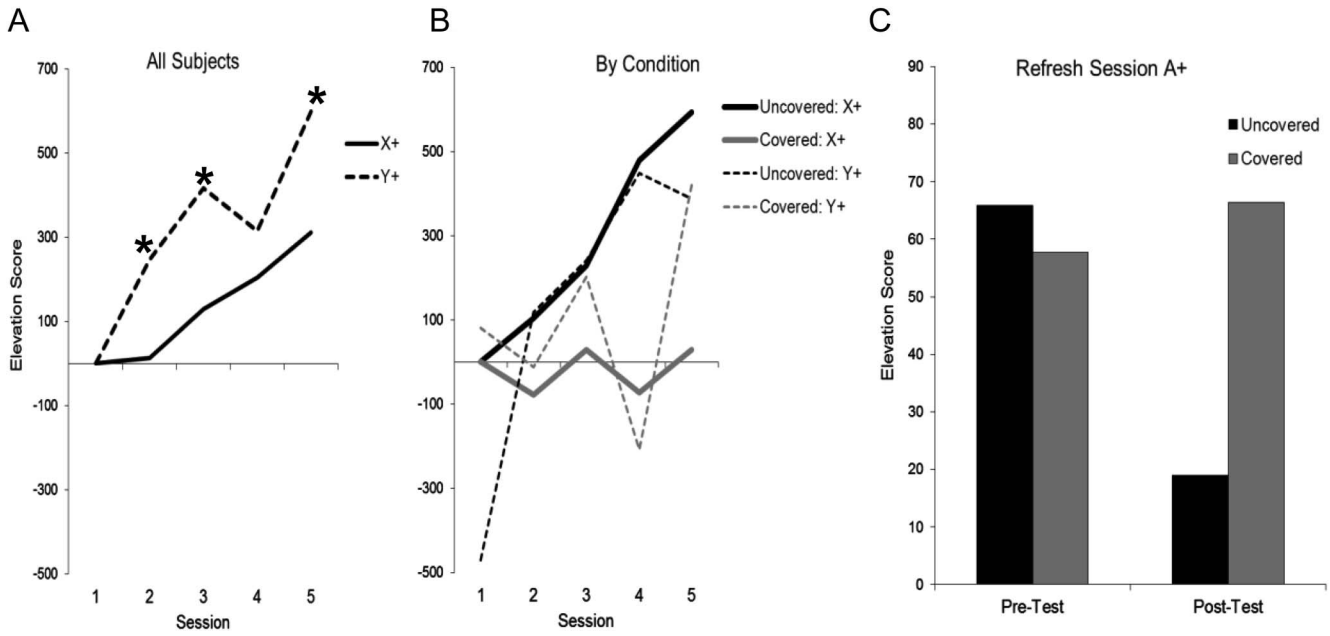

Figure 7. Mean elevation scores (nose poke duration during CS—nose poke duration before CS) normalized to first session during Retardation-of-Acquisition test, '*' reflect differences at the .05 level of significance. Panel A shows combined results for all subjects. Responses to Y increased significantly across sessions, while responses to the putative inhibitor, X, did not change significantly. Panel B illustrates mean responses to X+ (solid lines) and Y+ (dashed lines) trials across the five retardation sessions for subjects previously tested with X Uncovered (black lines) or Covered (gray lines). Despite equivalent performance on the first session, only subjects that previously experienced the X absent test while X was Uncovered showed a significant increase in responses to X across the retardation sessions. These subjects also showed a significant reduction in responses to the first A+ trial of the refresher session that preceded retardation and followed the X absent test (C).

compared with A-alone trials from training (when the nonoccurrence of X was unambiguous). Responses to B, on the other hand, did not differ from training, regardless of the status of X at test (Covered or Uncovered).

Notably, the summation effect demonstrated to A when X was covered was weaker than demonstrated during the preceding training and summation test. This is consistent with the magnitude of behavioral change demonstrated in our prior experiments (Fast & Blaisdell, 2011) and in mediated conditioning procedures relying on CS-evoked images, suggesting that an evoked representation may be weaker, or distinguishable, from the physical presentation of a cue (consider Dickinson & Burke, 1996; Holland, 1983; Wagner, 1981 for formalized accounts of this effect). Others (e.g., Holland, 1990; Konorski, 1948, 1967) have argued that rats, like humans, distinguish between images and reality. This distinction may occur on the basis of additional activity generated in the nervous system when physical sensation occurs. It should, therefore, not be surprising that rats respond with less vigor when guided by retrieved representations compared with a cue physically perceived through the senses.

Experiment 2 provides strong evidence that rats behave according to a retrieved representation, or image, of a relevant stimulus that has been blocked from physical detection because there was a selective reduction in responding to only A when the inhibitor (X) was ambiguously absent. However, the lack of inhibitory transfer to B when X was covered might still be explained in terms of a configural approach to the training and testing cues. It is possible that responses to A when X was covered were driven by generalization from both A+ and AX− training trials. On the other hand, responses to B when X was covered could only be driven by generalization from B+ training trials. In other words, nonreinforced AX− trials may more closely resemble A-alone test trials when X is covered than B-alone trials when X is covered. Given that generalization is driven by similarity, it is possible that greater inhibition from AX− training trials generalized to the more similar A-alone than to the less similar B-alone test trials with X covered. Nonetheless, simulation of Pearce's (1994) configural model fails to produce this pattern of results. Furthermore, it is unclear how a configural-generalization model could account for the successful summation performance of both groups along with the unanticipated, and subtle, group differences in the subsequent retardation-of-acquisition test.

Despite both groups experiencing identical conditioned inhibition training and summation test performance, only subjects tested on A and B with X Covered during the X absent test showed evidence of retarded acquisition of an excitatory association to X. In other words, X's inhibitory association had somehow been attenuated or extinguished in Group Uncovered, while it was maintained for Group Covered. The difference in retardation-of-acquisition performance may be attributable to the position of the cover during the X absent test because subjects otherwise received identical training and test stimuli. More important, sensory expe-

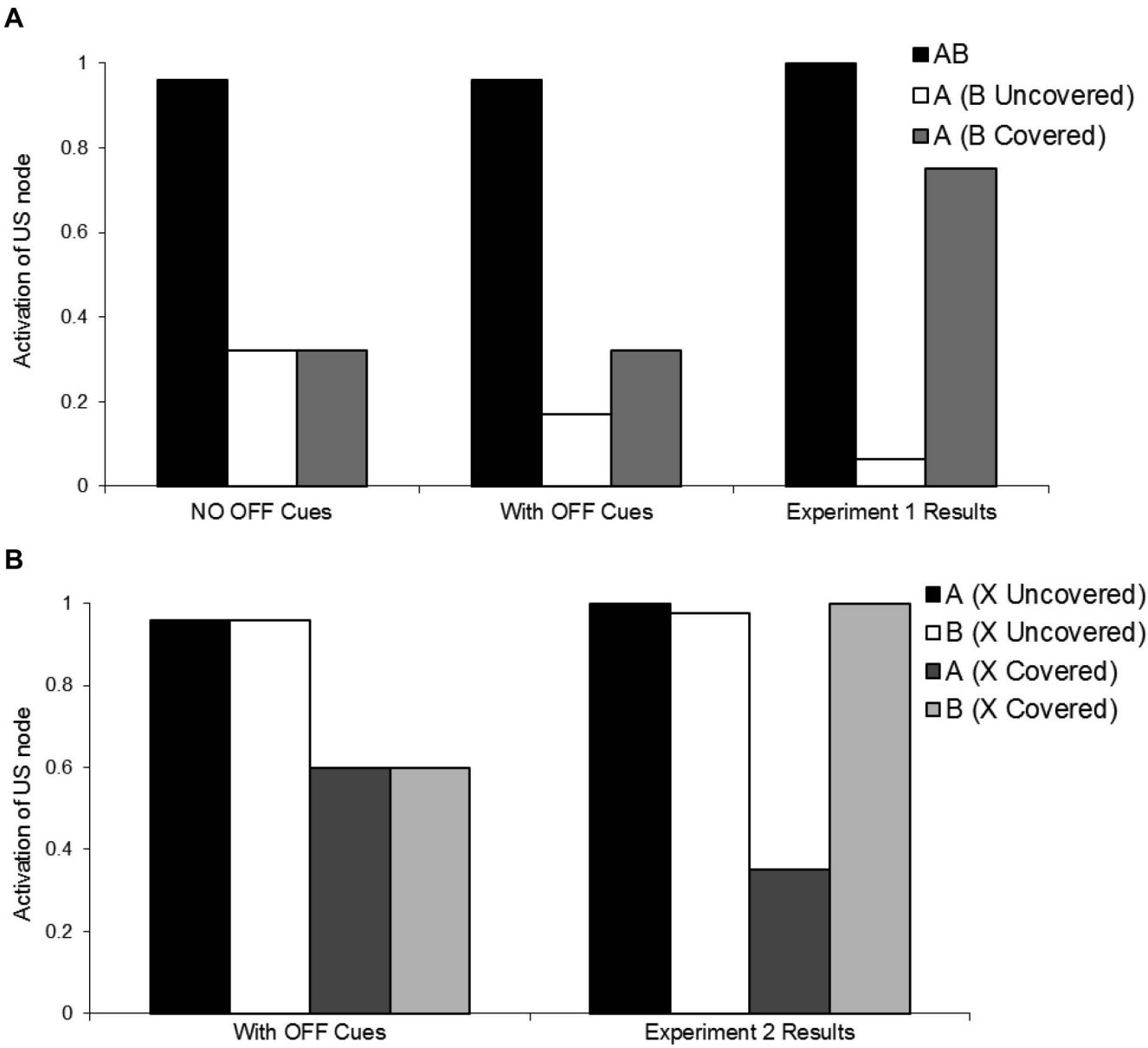

Figure 8. Simulations of Pearce's (1994) configural theory. (A) Experiment 1 simulation with standard convention to include only present cues (left; AB+, A−; '+' and '−' refer to the presence and absence of the US, respectively) and explicitly OFF representations of cues (middle) as suggested by Dwyer and Burgess (2011). During training, the AB compound is represented as $A_{ON}B_{ON}+$. Test trials with B Uncovered and unlit are represented as $A_{ON}B_{OFF}-$, while test trials with B Covered are represented as $A_{ON}-$. When OFF cues are included, the simulation accurately predicts Experiment 1 results (standardized to max value for scaling, right). (B) Simulation of Experiment 2 using OFF cues (left). Training was represented as $A_{ON}X_{OFF}+$, $B_{ON}X_{OFF}+$, and $A_{ON}X_{ON}$-. Although the simulation accurately predicts reduced responding to A when X is Covered, it erroneously predicts reduced responding to B when X is Covered. Thus, removing the signal value of explicitly absent cues cannot account for the results of Experiment 2 (standardized to max value, right).

riences during the X absent test did not differ between the groups; that is, both groups experienced separate trials with only A and B physically presented during the X absent test. To understand how this experience could extinguish X's inhibition, it is necessary to consider how inhibition is extinguished under normal circumstances. Zimmer-Hart and Rescorla (1974) found no attenuation in inhibition after presenting the inhibitor independently without the US (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972); however, others (Hallam, Matzel, Sloatt, & Miller, 1990; Lysle & Fowler, 1985; Miller & Schachtman, 1985; Stout & Miller, 2007) observed reduced inhibition by extinguishing the excitatory cue with which the inhibitor had been associated. Thus, it is possible

that nonreinforced probe trials of A when X was explicitly absent (Uncovered) during the X absent test resulted in some extinction of A that likewise reduced the inhibition of X. Indeed, these subjects responded significantly less to A-alone trials during the refresh training session that followed the X absent test.

Given that both groups experienced A-alone probe trials during the X Absent Test, why would extinction to A only occur for subjects tested when X was explicitly absent (Uncovered)? Others (Rescorla, 2003; Soltysik, 1985; Soltysik, Wolfe, Nicholas, Wilson, & Garcia-Sanchez, 1983) have shown excitatory associations are maintained when extinction trials (cue presentations without the US) occur in the presence of an established conditioned inhibitor. Although the inhibitor, X, was not *explicitly* present when Covered during the X absent test, the reduced CRs to A strongly indicate these rats acted *as if* guided by a representation of X. Given X showed signs of retarded acquisition of an excitatory association for these subjects, the image of X seems sufficient to protect A from extinction during probe trials without the US (and likewise protect itself from extinction). This may qualify as a mediated protection-from-extinction effect, similar to other forms of mediated learning. Given the lack of power in our retardation test, this effect warrants further empirical scrutiny. Nonetheless, these results are consistent with and support our conclusion that rat behavior when a cue is occluded from perception is driven not by the removal of a cue (as proposed by Dwyer & Burgess, 2011), or generalization of a configural representation, but by the presence of an associatively retrieved representation of the perceptually absent event.

Collectively, our results demonstrate associative learning mechanisms not only provide knowledge, but also provide the foundation for resolving information-poor situations through associatively retrieved representations. A retrieved representation may simply be activity in the nervous system uncorrelated with direct experience through the sensory organs (i.e., memory as opposed to sensory). This, of course, may not necessarily invoke a mental image as we may experience when we, as humans, imagine something that is not physically present (cf., O'Craven & Kanwisher, 2000). Nonetheless, our results suggest that rats may use representations in a manner similar to what humans describe as imagination (Barron, Dolan, & Behrens, 2013) to enable predictions about situations that have never been experienced. Such processes of imagination underlie the ability to entertain possible alternative realities about the state of the world that subserve hypothetical and counterfactual reasoning as the basis for scientific and philosophical thought. This research, therefore, has interesting implications for the evolutionary origins of source monitoring—the ability to distinguish between actual and imagined events (Johnson, Hashtroudi, & Lindsay, 1993). The neural mechanisms involved in the current study may be homologous to those responsible for source monitoring and its failures in humans (Schacter, Guerin, & St. Jacques, 2011). Better understanding these neural mechanisms may therefore afford clinical benefits.

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