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BRIEF REPORT

Rats are sensitive to ambiguity

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Abstract In the present study, we investigated response decisions made under conditions of incomplete information in rats. In Experiment 1, rats were trained on either a positive patterning (PP; A-, B-, AB+) or a negative patterning (NP; A+, B+, AB-) instrumental lever-press discrimination. Subjects that had learned an NP discrimination responded less to Cue A when Cue B was covered at test. The cover did not, however, affect test responses to Cue A in the PP condition. In Experiment 2, rats received concurrent training on both PP and NP discriminations. After concurrent training, responses to Cue A were different with B covered versus uncovered for both NP and PP discriminations. We discuss possible accounts for why exposure to a nonlinearly soluble discrimination (NP) may have affected sensitivity to cue ambiguity produced by the cover. These results have interesting implications for representational processes engaged in problem solving.

Keywords Positive patterning · Negative patterning · Problem solving · Ambiguity · Incomplete information

Studies of associative learning have shown that nearly every member of the animal kingdom, from honeybee to human, can learn about patterns of events that occur in the world. Pattern learning is most notable in Pavlovian and instrumental conditioning studies involving compounds of multiple cues. In a positive patterning (PP) discrimination (A-, B-, AB+), for example, an outcome is delivered whenever two cues, A and B, are presented simultaneously (AB+), but not when only one of the two cues is present (A-, B-). Similarly, in a negative patterning (NP) procedure (A+, B+, AB-), the elements presented alone are rewarded (A+, B+), but the compound is not (AB-). Rats readily learn to discriminate the set of cues that predict a food outcome from those that predict no food (Holland, 1989; Rescorla, 1972).

What is unknown, however, is how the rat would respond when only partial information about the cues is available. For example, after learning a PP discrimination involving rewarding two light cues—A and B—with food, the rat's behavior should reflect anticipation of the food when both A and B are present but not when either A or B are presented alone. How will the rat react to the presentation of A if the bulb on which B had been presented during training is covered by an opaque shield at test? One possibility is that the rat responds only to stimulus events in binary terms as being present or absent, and thus would respond on this trial as if only A were present (which accords with the contingencies experienced during training) and would therefore not look for food. Alternatively, the rat could be sensitive to the change in the stimulus situation of B being occluded from view and represent B as possibly being present despite being obscured. In this case, where the status of B (present or absent) is ambiguous, the rat may respond as if B were present and look for food at a greater rate than would be predicted on the basis of the training contingencies on trials with A alone. A third possibility is that feeder activity may be at intermediate levels between rates elicited on AB or on A alone trials. In this scenario, the rat would again demonstrate sensitivity to the ambiguous nature of B, but would behave *as if* it is uncertain as to whether B is present

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underneath the shield. Note that although we speak of the rat as being uncertain about the status of B when covered, or as being sensitive to whether B is covered at test, we do not necessarily imply that the rat has an *awareness* of these conditions. Rather, as is typical of rational accounts of behavior, we are using these terms in a functional sense rather than in terms of the subjective experience of the subject (Clayton, Emory, & Dickinson, 2006; Kacelnik, 2006). The following experiments addressed this question.

Experiment 1

Rats learned either a PP or a NP discrimination involving two lights, A and B. We employed an instrumental conditioning procedure in which rats had to press a lever to receive a food reward. After subjects learned to successfully discriminate between the elemental (A or B) and compound (AB) trials, they were tested on A-alone trials with B either covered by an opaque shield (ambiguous) or uncovered and unlit (explicit). Performance to A at test may be adversely affected by the introduction of the novel cover at test (Bouton, 2004). To control for such a generalization decrement account of changes in performance introduced by the cover at test, the cover was also present in the chamber on uncovered test trials, but was positioned centrally on the chamber wall between lights A and B so that it did not obscure B.

Table 1 Experiment 1 design

Condition	Phase 1	Test
PP-covered	A- / B- / AB+	A- with B covered
PP-uncovered	A- / B- / AB+	A- with B uncovered
NP-covered	A+/ B+/ AB-	A- with B covered
NP- uncovered	A+/ B+/ AB-	A- with B uncovered

A and B are 30-s lights. "Covered" and "uncovered" indicate whether or not B's bulb was covered at test. "+" = reinforcement delivered for lever presses occurring during the discriminative stimulus on a VR-4 schedule; "-" = no reinforcement; "/" separates trial types presented within the same session. *PP* positive patterning *NP* negative patterning

Method

Subjects Seventy-four experimentally naive female Long–Evans food-restricted (to 85% ad lib weight) rats (*Rattus norvegicus*) acquired from Harlan (Indianapolis, IN) served as subjects. Subjects were pair-housed in transparent plastic tubs with a wood shaving substrate in a vivarium maintained on a reverse 12-hr light/dark cycle. Experiments were run during the dark portion of the cycle. Rats were randomly assigned to one of four groups (*n*s = 18, 18, 19, and 19, respectively): PP-covered, PP-uncovered, NP-covered, or NP-uncovered (see Table 1).

Apparatus Ten experimental Med Associates (Georgia, VT) chambers, measuring 30 x 25 x 20 cm (L x W x H) were used for this and for the following experiment. Each chamber was housed in a sound and light insulating chest. The chamber had Plexiglas front and back walls and ceiling, aluminum side walls, and stainless-steel rod floors.

Each chamber had a water dipper to deliver sucrose solution (20%) reinforcement into a drinking niche. Head entry into the drinking niche was monitored by an infrared beam and photo detector aligned across the niche opening. A 3.5-cm wide operant lever was positioned 1 cm to the left of the food niche on the metal wall. A diffuse LED located 9 cm to the right of the food niche could be flashed at a rate of 2 Hz to serve as A or B, counterbalanced. A 28-V incandescent bulb located 9 cm to the left of the food niche served as B or A, counterbalanced (Fig. 1A). A 4-cm black plastic square cover, designed to mimic a covered light bulb, was affixed to a 7.8-cm x 4.1-cm aluminum plate. Stimuli (A, B, or AB) were presented for 30 s.

Procedure The procedures used are explained as follows.

Magazine training. All sessions terminated after 60 min with a mean intertrial interval (ITI) of 70 s (unless otherwise noted). On Day 1, rats were trained to drink from the dipper containing sucrose solution delivered every 20 ± 15 s.

Lever-press shaping. On Days 2–6, rats were reinforced with 10-s access to a sucrose solution for lever pressing. During the first two sessions, each lever press was reinforced (CRF). In addition, reinforcement was delivered every 120 s. During the next three sessions, an average of one of every four lever presses was reinforced on a variable ratio (VR-4) schedule.

Patterning training. Rats received 12 A-alone, 12 B-alone, and 12 AB presentations per session. Trial order was quasirandom. For rats in the PP condition, lever presses made during presentations of A or B were not reinforced, whereas lever presses to the AB compound were reinforced with 5 s of sucrose on a VR-4 schedule. For rats in the NP condition, lever presses made during the A or B, but not during the AB compound, trials were reinforced. Reinforcement could be delivered multiple times on a given trial. Rats received daily training sessions until they met the performance criterion defined below. Feeder activity and lever pressing were recorded during a 30-s period before the start of each trial and during each 30-s trial.

A discrimination ratio (DR) was calculated by subtracting mean elevation score (trial – pretrial responses) on non-reinforced trials from mean elevation score on reinforced trials and dividing by mean elevation scores across all trial types. For example, for PP, the discrimination score = [mean AB – (mean A + mean B)/2]/[mean AB + (mean A + mean B)/2]. Given this calculation, DR scores could range between −1 and +1

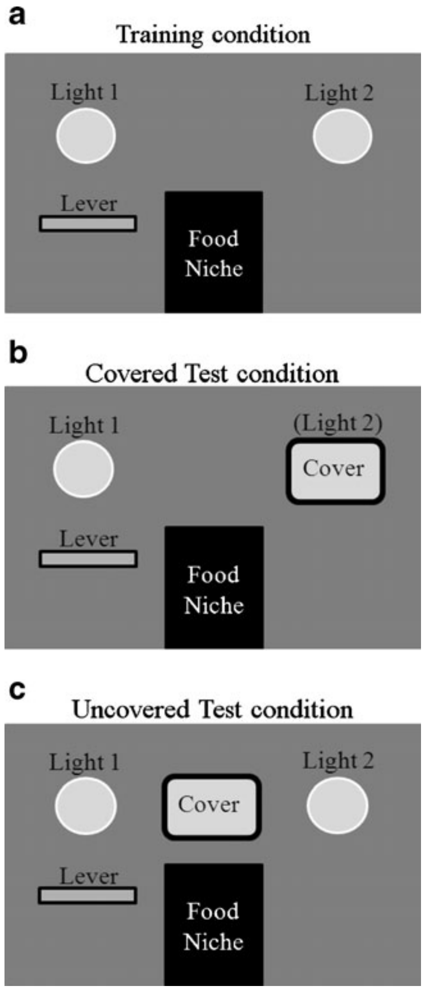

Fig. 1 **a** The stimulus configuration during training. Lights 1 and 2 represent Cues A and B, counterbalanced within group. **b** and **c** The chamber layout during test sessions with B covered (**b**) or uncovered (**c**). Fig. 1. Schematic of experimental chamber wall

with a score of 0 representing no discrimination and +1 = perfect discrimination. A DR greater than .65 on three of five consecutive sessions was used as threshold to move subjects on to testing. Rats failing to meet criterion after 66 sessions were moved to testing to avoid overtraining effects (e.g., Yin, Knowlton, & Balleine, 2004). One subject was removed from the study for health reasons.

Test A. In each 20-min test session, rats received 12 nonreinforced 30-s presentations of A. In this session, half of the rats were tested with B covered with a plastic cover (Fig. 1B); the remaining half were tested with B uncovered, but the plastic cover placed next to B's bulb (Fig. 1C).

Results and discussion

Subjects in both the PP and NP conditions learned the discrimination between reinforced and nonreinforced trial types during acquisition (Fig. 2A). A mixed ANOVA was calculated on mean elevation scores for the elemental (A and B) and compound (AB) trial types from the final session of acquisition between the PP and NP patterning conditions, revealing a significant interaction between trial type and patterning, $F(1, 71) = 617.94$, $p < .001$, $d = 49.72$. Subsequent planned comparisons revealed that the PP condition responded at a significantly higher rate to the compound trials than to the elemental trials, $F(1, 34) = 505.49$, $p < .001$, $d = 44.97$, as was predicted. Also as was predicted, the NP condition responded at a significantly higher rate to the elemental trials than to the compound trials, $F(1, 37) = 213.36$, $p < .001$, $d = 29.21$. The patterning conditions also differed significantly in their response rates on elemental trials, $F(1, 71) = 272.98$, $p < .001$, $d = 33.04$, and on compound trials, $F(1, 71) = 202.86$, $p < .001$, $d = 28.49$, consistent with the stimulus

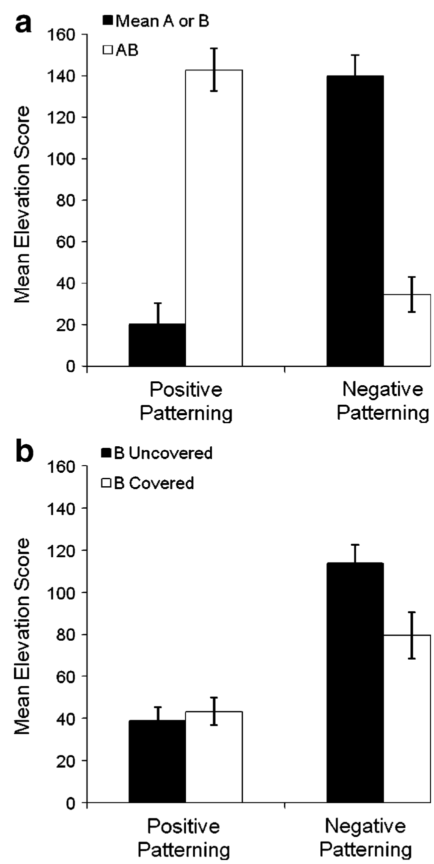

Fig. 2 **a** Mean elevation scores from the final session of pattern discrimination training in Experiment 1. Successful positive patterning (PP) discrimination is shown as higher response rates on compound (AB) trials than on elemental trials (A or B). Successful negative patterning (NP) discrimination is shown as higher response rates on element trials (A or B) than on compound (AB) trials. **b** shows mean elevation scores from trials with Cue A from the first test session. Subjects in Group NP lever pressed more during Cue A with B uncovered than when B was covered. Subjects in Group PP showed equally low rates of lever pressing during Cue A with B covered or uncovered. *Error bars* represent the standard errors of the means

contingencies of patterning training wherein elemental trials (A or B) are reinforced for NP but not for PP, and compound (AB) trials are reinforced for PP but not NP.

Test results are presented in Fig. 2B. Covering B's light at test produced a drop in lever pressing during A in the NP condition (baseline responses did not differ: NP-covered, $M=13$, $SD=19.54$; NP-uncovered, $M = 30$, $SD = 74.15$; $t(36) = -0.99$, $p > .05$), but had no effect in the PP condition (although baseline responses also did not differ between PP-covered, $M = 16$, $SD = 24.45$; and PP-uncovered, $M = 11$, $SD = 11.00$; $t(33) = 0.83$, $p > .05$). An ANOVA conducted on mean elevation scores with patterning (PP and NP) and trial type (B covered or B uncovered) as factors revealed a main effect of patterning, $F(1, 69) = 258.34$, $p < .001$, $d = 32.15$ (consistent with the differences found between the conditions on elemental trials at the conclusion of training as described above), and a significant Patterning x Trial Type interaction, $F(1, 69) = 5.11$, $p = .02$, $d = 4.52$. Planned comparisons revealed that the NP condition responded at a significantly higher rate than the PP condition when B was uncovered, $F(1, 69) = 37.42$, $p < .01$, $d = 12.23$, and when B was covered, $F(1, 69) = 8.96$, $p < .01$, $d = 5.99$. The NP condition also responded significantly less when B was covered than when it was uncovered, $F(1, 69) = 8.38$, $p < .01$, $d = 5.79$. Response rates of the PP condition, however, did not differ between the two test trial types, $F(1, 69) < 1.0$, $d = 0.70$.

Experiment 2

Why did covering B's light affect lever pressing during A in the NP condition but not in the PP condition? Although PP and NP discriminations are procedurally similar, their solutions are computationally dissimilar. Positive patterning is a linearly separable problem (e.g., Bush & Mosteller, 1951; Jenkins & Ward, 1965; Rescoral & Wagner 1972; Wagner & Rescorla, 1972); in other words, it is possible to solve a positive patterning discrimination through simple summation of the weak, subthreshold associations to each nonreinforced elemental cue when they are presented together, thereby reaching a response threshold. Negative patterning, on the other hand, requires a nonlinear solution, such as that provided by an exclusive-or (XOR) logical structure, in which reward is conditional on the presence of one and only one element, and does not occur when multiple elements are present (Grand & Honey, 2008; Medin, Altom, Edelson, & Freko, 1982; Medin & Smith, 1981; Smith et al. 2010), or on a configural solution (Bellingham, Gillette-Bellingham, & Kehoe 1985; Deisig, Lachnit, Giurfa, & Hellstern, 2001; Kehoe & Graham, 1988; Lachnit & Lober, 2001; Lachnit, Ludwig, & Reinhard, 2007; Ludwig & Lachnit, 2003; Pearce, 1994). Perhaps sensitivity to ambiguity requires exposure to nonlinear problems (configural or XOR). Indeed, Williams and Braker (1999, 2002) and Mehta and Williams (2002) have shown that the extent to which people rely on elemental or configural processes to solve problems differs both as a function of the task and prior training. Alvarado and Rudy (1992) have also provided evidence that configural solutions can transfer to tasks that are normally learned elementally. It is therefore possible that prior training with a simple linear task such as positive patterning fails to influence how the rats approach the ambiguous situation at test in the same way that rats that previously learned negative patterning using configural or XOR strategies approach the same ambiguous situation. Experiment 2 was designed to test this hypothesis by training subjects concurrently on both PP and NP discriminations. If exposure to a nonlinear problem, such as an NP discrimination, is necessary for sensitivity to subsequent cue ambiguity, then subjects tested afterward on the PP discrimination should be sensitive to the presence or absence of the cover.

We used a procedure similar to that of Experiment 1, with the addition that subjects were exposed to both PP and NP discriminations. Auditory cues were used for the additional patterning discrimination due to equipment limitations. Half of the subjects learned a visual PP (A-, B-, AB+) and an auditory NP (C+, D+, CD-) discrimination; the remainder learned a visual NP (A+, B+, AB-) and an auditory PP (C-, D-, CD+) discrimination. Subjects were then tested on A alone with B either covered or uncovered.

Method

Subjects Forty experimentally naive female Long–Evans rats (*Rattus norvegicus*) that were maintained as in Experiment 1 were randomly assigned to one of four conditions (*n*s = 10): PP-covered, PP-uncovered, NP-covered, or NP-uncovered (Table 2).

Table 2 Experiment 2 design

Condition	Phase 1	Test
PP-covered	A- / B- / AB+ / C+ / D+ / CD-	A- with B covered
PP-uncovered	A- / B- / AB+ / C+ / D+ / CD-	A- with B uncovered
NP-covered	A+/ B+/ AB- / C- / D- / CD+	A- with B covered
NP-uncovered	A+/ B+/ AB- / C- / D- / CD+	A- with B uncovered

A and B are 30-s lights; C and D are 30-s auditory cues. "Covered" and "uncovered" indicate whether or not B's bulb was covered at test. "+" = reinforcement delivered for lever presses occurring during the discriminative stimulus on a VR-4 schedule; "-" = no reinforcement; "/" separates trials within the same session. *PP* positive patterning, *NP* = negative patterning

Apparatus Sixteen experimental chambers similar to those used in Experiment 1 were used. Additionally, one speaker located on the rear wall of the chamber delivered a high-frequency tone (T; 3,000 Hz) 8 dB(A) above background (62 dB), and another speaker on the ceiling of the chamber delivered a click train (4/s) 8 dB(A) above background. The tone and click train served as discriminative stimuli C and D, counterbalanced within condition. A 4-cm square chew-resistant stainless steel cover replaced the black plastic square cover used in Experiment 1.

Procedure The procedures used are explained as follows.

Magazine and lever-press training. This was the same as in Experiment 1, except that two additional CRF sessions were given.

Patterning training. All rats received six A-alone, six B-alone, and six AB compound presentations; in addition to six C-alone, six D-alone, and six CD compound presentations that were quasirandomly presented within each session. PP discriminations involved reinforcing lever presses made during compounds (AB or CD) but not during elements (A, B, C, or D). NP discriminations involved reinforcing lever presses made during elements but not during compounds. All other methods were the same as those used in Experiment 1.

Days 12–61. The lever press response-reinforcer contingency was gradually increased across sessions from a CRF to a VR-4 schedule of reinforcement. Each rat moved on to testing as soon as its discrimination performance reached a DR at or above 0.5 on both visual and auditory PP and visual NP discriminations, and a DR at or above 0.2 on auditory NP discriminations on three out of five consecutive sessions and during the two most recent sessions. A lower DR was used for the auditory NP discrimination because it was a more difficult discrimination for subjects to master. It was, nevertheless, effective in training a discrimination (see the Results section). These same subjects were also still required to meet or exceed a DR of .5 on the visual PP discrimination that they would later be tested on. Five subjects (two PP covered, one PP uncovered, one NP covered, and one NP uncovered) that failed to meet this criterion were eliminated from the study.

Test A. Testing on visual cue A was conducted as described in Experiment 1, except that six presentations of A were given in a single 10-min test session

Results

Subjects in the visual NP/auditory PP conditions (NP covered and NP uncovered) acquired the discriminations in fewer sessions ($M = 55$, $SD = 15$) than did subjects in the visual PP/auditory NP conditions (PP covered and PP uncovered; $M = 73$, $SD = 11$), $F(1, 33) = 16.64$, $p < .01$, $d = 8.16$. Nevertheless, all subjects acquired the discrimination (Fig. 3). A mixed ANOVA calculated on the final-session elevation scores for the six trial types (A, B, AB, C, D, CD) between patterning (PP and NP) revealed main effects of trial type, $F(5, 165) = 7.39$, $p < .01$, $d = 5.44$, and patterning, $F(1, 33) = 360.68$, $p < .01$, $d = 37.98$, and their interaction, $F(5, 165) = 210.81$, $p < .01$, $d = 29.04$. Planned comparisons revealed successful visual PP, auditory PP, visual NP, and auditory NP discriminations, $Fs(1, 132) >= 38$, $ps < .01$, $ds >= 12.44$. Thus, all subjects successfully learned the concurrent PP and NP discriminations, regardless of stimulus modality (a finding that also supports our selection of test criterion as described above).

Test results are presented in Fig. 4. Replicating the results of Experiment 1, subjects in the NP-uncovered condition responded more during Cue A than did subjects in the NP-covered condition (although baseline responses did not differ: NP-uncovered, $M = 6$, $SD = 5.24$; NP covered, $M = 6$, $SD = 3.43$; $t(15) = -0.21$, $p > .05$). Unlike

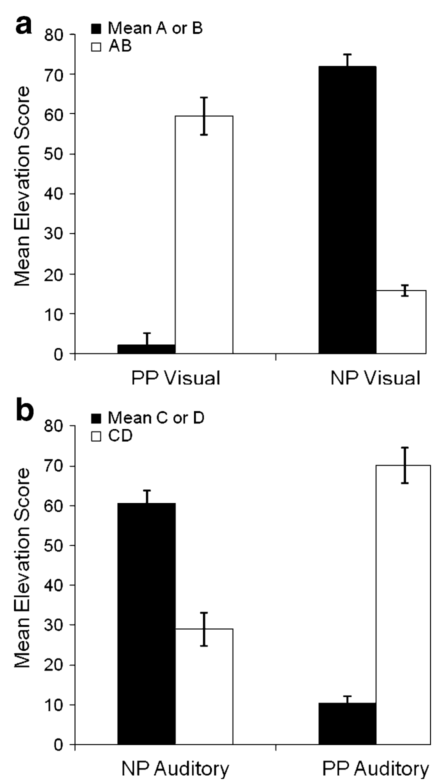

Fig. 3 Mean elevation scores from the final session of pattern discrimination training in Experiment 2 for the visual discriminations (**a**) and the auditory discriminations (**b**). Successful positive patterning (PP) discrimination is shown as higher response rates on compound (AB or CD) trials than on elemental trials (A, B, C, or D). Successful negative patterning (NP) discrimination is shown as higher response rates on element trials (A, B, C, or D) than on compound (AB or CD) trials. *Error bars* represent the standard errors of the means

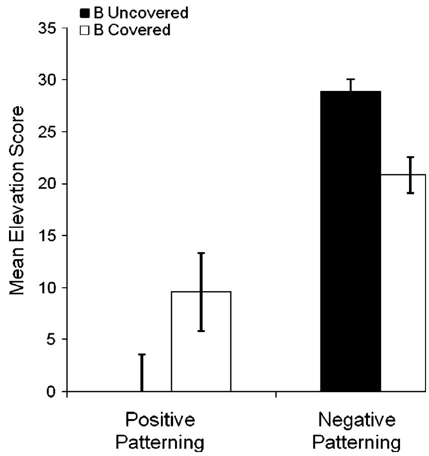

Fig. 4 Mean test results from trials with Cue A from the first test session of Experiment 2. Subjects in Group Negative Patterning (NP) lever pressed more during Cue A with B uncovered than when B was covered. Subjects in Group Positive Patterning (PP) showed more lever pressing during Cue A with B covered than when B was uncovered. *Error bars* represent the standard errors of the means

in Experiment 1, the cover also made a difference to responses in the PP conditions, with subjects in the PP-uncovered condition responding less to Cue A than did subjects in the PP-covered condition during test trials (baseline responses also did not differ between the PP conditions: PP-uncovered, M = 19, SD = 18.69; PP-covered, M = 10, SD = 10.06; $t(15) = -1.22$, $p > .05$). These observations were supported by a two-way ANOVA conducted on elevation scores with patterning (PP and NP) and test trial type (covered and uncovered) as factors, which revealed a main effect of patterning, $F(1, 31) = 55.13$, $p < .001$, $d = 14.85$, and a Patterning x Trial Type interaction, $F(1, 31) = 10.65$, $p = .003$, $d = 6.53$. Planned comparisons revealed that the PP-uncovered condition responded significantly less than the NP-uncovered condition, $F(1, 31) = 58.91$, $p < .01$, $d = 15.35$, demonstrating positive and negative patterning discriminations. Moreover, responding in the NP-covered condition was lower than in the NP-uncovered condition, $F(1, 31) = 4.55$, $p < .05$, $d = 4.27$, thereby replicating the effect of the cover on NP discrimination from Experiment 1. Finally, responding in the PP-covered condition was greater than that in the PP-uncovered condition, $F(1, 31) = 6.15$, p < .02, $d = 4.96$, revealing an effect of the cover on PP discrimination, unlike in Experiment 1. Thus mere exposure to an NP discrimination rendered the positive patterning discrimination sensitive to cue ambiguity produced by the cover in this experiment.

General discussion

After successfully learning a PP or an NP discrimination involving visual cues in Experiment 1, only subjects that learned an NP discrimination were affected by the presence or absence of a cover over Cue B on responding to Cue A at test. Exposure to an auditory NP discrimination, however, induced sensitivity to the cover in the PP condition (Experiment 2). Collectively, the results from Experiments 1 and 2 indicate that rats are sensitive to ambiguity in cue information and suggest factors that may influence this sensitivity.

These results are consistent with other work from our lab that has shown rats to be sensitive to an event that is explicitly absent as compared with when its absence is ambiguous. Blaisdell,, Leising, Stahlman, and Waldmann, (2009) trained rats on a Pavlovian sensory preconditioning task in which they first learned that a tone signaled a light in Phase 1 treatment, and then learned that the light signaled food in Phase 2 treatment. At test, the tone was presented either with the light bulb present but unlit or physically removed from the chamber (or covered; Blaisdell & Waldmann, in press). Rats evinced much greater feeder activity with the bulb absent than with it present. That is, rats behaved as if they understood that with the bulb uncovered they should be able to see the light (which was predicted by the tone), whereas when the bulb was absent or covered they behaved as if they understood that they could not determine the status of the light. When the light was explicitly absent at test, rats did not search for food when tone was presented. When the status of the light was ambiguous, however, they acted as if the light was present and searched for food. Sensitivity to ambiguity shows that rats act as if they understand that environmental conditions can perceptually mask extant events. Moreover, rats appear to discriminate the conditions under which an event should or should not be observable.

A noteworthy outcome from our present experiments was that this sensitivity can be modulated by the training history of the rat. This is consistent with results found in humans, (e.g., Mehta & Williams, 2002; Williams & Braker, 1999, 2002). What is unclear, however, is the nature of the mechanism mediating these effects. The fact that covering B's lamp at test affected the PP condition only when subjects had also had experience with an NP discrimination suggests some possibilities and rules out others.

We can rule out an account in terms of generalization decrement between training and testing conditions produced by the cover. According to this account, the reason for the change in performance in tests of A with the cover present relative to performance with the cover absent (or in a different location within the chamber) is due to the presence of the cover over B's location constituting a contextual change. Although contextual changes can disrupt the expression of learned behavior and thereby degrade performance (Bouton, 2004), this explanation fails to account for the different effects of the cover on PP discriminations between Experiments 1 and 2 and the consistent effect on NP across both experiments.

Another explanation is in terms of the computational complexity of the discrimination. Following the results of Experiment 1, we hypothesized that exposure to only linearly soluble PP discrimination failed to engage sensitivity to cue ambiguity. It is possible, therefore, that sensitivity to stimulus ambiguity requires exposure to nonlinearly separable problems, such as the NP discrimination. Data from Experiment 2 support this. Rats showed sensitivity to the presence or absence of the cover at test on the PP discrimination after having also been exposed to an NP discrimination. It is also possible that NP and PP discriminations normally rely to different extents on configural processing. In accordance with Alvarado and Rudy (1992), it is possible that exposure to concurrent PP and NP discriminations engages configural processing to the PP discrimination, whereas exposure to the PP discrimination alone engages primarily an elemental process. It remains unclear, however, whether exposure to a nonlinear or configural discrimination is necessary, or whether mere exposure to any difficult discrimination—even if soluble by a linear operation—would be sufficient. A further possibility, suggested by a reviewer, is that the inclusion of a second patterning discrimination using auditory cues affected the salience of the unilluminated bulbs in a way that increased the perceptual discrepancy between the presence versus absence of the cover at test. It is yet to be determined the actual mechanism involved in this sensitivity to ambiguity in a situation, but it very likely could reflect bottom-up associative processes (Danks, 2008) or top-down cognitive processes (Blaisdell & Waldmann, in press).

Finally, differences in the relative ratio of reinforced to nonreinforced trials during acquisition may also account for the difference between experiments (e.g., Lachnit et al., 2007; Lachnit et al. 2002). In Experiment 1, NP discriminations were reinforced on two-thirds of all trials, whereas PP discriminations were reinforced in only one-third of all trials during acquisition. Perhaps the greater proportion of reinforced trials increased sensitivity to cue ambiguity. This explanation is consistent with the results of Experiment 2 in which all subjects experienced a 50% rate of reinforcement during acquisition, which was a higher ratio of reinforced to nonreinforced trials in the PP discrimination (but a lower ratio for the NP discrimination) of Experiment 1. Lachnit et al. 2007 reported, however, that increasing the amount of reinforcement decreases responding in both a PP and an NP discrimination, whereas decreasing the amount of reinforcement increases responding in both discriminations. Thus, the observation that Group PP responded more whereas Group NP responded less when cue B was covered is inconsistent with the general account of Lachnit et al. 2007 suggesting that reinforcement ratio does not play a role in the sensitivity to cue ambiguity observed in our procedure.

Although the precise mechanism remains unclear and is currently under investigation in our laboratory, our results demonstrate that rats show a remarkable sensitivity to the stimulus dimension of ambiguity versus explicitness of the status of a cue. Moreover, this sensitivity appears restricted to subjects that had been exposed to nonlinear problems. To our knowledge, this is the first demonstration of such a representational capacity in rats.

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