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Blocking in autoshaped lever-pressing procedures with rats

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Abstract Rats will approach and contact a lever whose insertion into the chamber signals response-independent food delivery. This "autoshaping" or "sign-tracking" phenomenon has recently attracted considerable attention as a platform for studying individual differences in impulsivity, drug sensitization, and other traits associated with vulnerability to drug addiction. Here, we examined two basic stimulus selection phenomena—blocking and overshadowing—in the autoshaped lever pressing of rats. Blocking and overshadowing were decidedly asymmetrical. Previously reinforced lever-extension conditioned stimuli (CSs) completely blocked conditioning to auditory cues (Exps. 1 and 2), and previously nonreinforced lever-extension CSs overshadowed conditioning to auditory cues. By contrast, conditioning to lever-extension CSs was not blocked by either auditory (Exp. 3) or lever-insertion (Exp. 4) cues, and was not overshadowed by auditory cues. Conditioning to a lever-insertion cue was somewhat overshadowed by the presence of another lever, especially in terms of food cup behavior displayed after lever withdrawal. We discuss several frameworks in which the apparent immunity of autoshaped lever pressing to blocking might be understood. Given evidence that different brain systems are engaged when different kinds of cues are paired with food delivery, it is worth considering the possibility that interactions among them in learning and performance may follow different rules. In particular, it is intriguing to speculate that the roles of simple cue–reinforcer contiguity, as well as of individual and aggregate reinforcer prediction errors, may differ across stimulus classes.

Keywords Associative learning · Autoshaping · Behavior systems · Blocking · Classical conditioning · Cue competition

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Rats will approach and contact a lever whose insertion into the chamber signals response-independent food delivery (Boakes, 1977; Flagel, Akil, & Robinson, 2009; Flagel, Watson, Akil, & Robinson, 2008; Kearns & Weiss, 2004; Tomie, 1996; Tomie, Grimes, & Pohorecky, 2008). This "autoshaping" or "sign-tracking" phenomenon has recently attracted considerable attention from neuroscientists, who have suggested that it reflects the endowment of the lever with "incentive salience," and that individual differences in these behaviors are correlated with individual differences in impulsivity, drug sensitization, and other traits associated with vulnerability to drug addiction (e.g., Flagel et al., 2009; Flagel et al., 2010; Flagel et al., 2008; Robinson & Flagel, 2009; Tomie et al., 2008).

Recent work from our laboratory shows important differences in the brain systems engaged in rats' autoshaped lever pressing and other seemingly closely related consequences of pairing initially neutral stimuli with food reinforcers. Although rats also come to approach and/or contact localized visual stimuli that are paired with food (Cardinal et al., 2002; Holland, 1977), the pattern of brain lesion effects on these various examples of sign tracking differed considerably. For example, although acquisition of conditioned approach to visual cues is prevented by lesions of the amygdala central nucleus but unaffected by lesions of the basolateral amygdala (Holland & Gallagher, 1999; Parkinson, Robbins, & Everitt, 2000; Parkinson, Willoughby, Robbins, & Everitt, 2000), autoshaped lever pressing is disrupted by lesions of the basolateral amygdala but unaffected by amygdala central nucleus lesions (Chang Wheeler, & Holland, Chang et al. 2012a, 2012b; but see Blundell, Hall, & Killcross, 2003).

Here we examined mutual blocking and overshadowing between auditory and lever-insertion stimuli paired with food, both to answer general questions about the occurrence of these important stimulus selection phenomena when different kinds of food signals are used, and to answer specific questions about the nature of learning in rat autoshaped lever pressing.

Blocking experiments might reveal differences in the content of learning about different conditioned stimuli (CSs). According to most learning theories, blocking occurs because, during compound conditioning, the reinforcer is already predicted on the basis of the pretrained cue. However, if two cues were predisposed to be associated with different aspects of a reinforcer, then prior conditioning to one of them might not interfere much with conditioning to the other (Holland, 1977; Rescorla, 1999a). Chang et al. (2012a, 2012b) suggested that lever-extension CSs might be especially associated with hedonic aspects of food, which would encourage consummatory responses. These aspects might not be associated with auditory or visual cues, which instead may be associated with more general incentive motivational properties of food. In that case, one might expect less blocking of lever pressing to lever cues by an auditory cue, as compared to blocking by another lever stimulus.

In light of a recent study by Costa and Boakes (2009), we paid particular attention to both lever-directed "sign-tracking" behaviors, and so-called "goal-tracking" (Boakes, 1977) responses, CS-evoked responses directed toward the food delivery site. Costa and Boakes found that although prior contextual conditioning interfered with subsequent acquisition of lever-directed responses to levers whose insertion was paired with food delivery, it did not interfere with the acquisition of goal-tracking responses to lever insertion. Contrasting these effects with those of other manipulations that interfered with both sign- and goal-tracking responses, they concluded that the context blocking effect on autoshaped lever-pressing reflected competition between sign- and goal-directed behaviors rather than true blocking of learning. Thus, here we examined both lever- and food cup-directed responding during lever presentations, as well as food cup responding after lever withdrawal, when lever pressing could not compete with goal-tracking responses.

In Experiments 1 and 2, we examined the blocking of conditioning to an auditory stimulus by a previously trained lever-extension CS, using between- and within-subjects designs, respectively. The design of Experiment 2 also permitted a between-subjects evaluation of overshadowing of conditioning to an auditory CS by a lever stimulus that had not been previously paired with food. Finally, we used the within-/between-subjects design of Experiment 2 to examine blocking and overshadowing of conditioning to a lever-extension CS by either an auditory CS (Exp. 3) or another lever-extension CS (Exp. 4).

Experiment 1

In Experiment 1, two groups of rats first received discrimination training in which extension of one lever was paired with food and extension of another lever was nonreinforced. Both groups of rats then received pairings of a white-noise + lever-extension compound with food delivery. The lever presented in this compound conditioning phase was the previously reinforced lever in Group BLK and the previously nonreinforced lever in Group OVR. Finally, responding to the noise alone was examined in all rats. Blocking of conditioning to the noise by a reinforced lever-extension CS would be inferred if responding to the noise was lower in Group BLK than in Group OVR.

Method

Subjects The subjects were 16 male Long-Evans rats (Charles River Laboratories, Raleigh, NC) that weighed 300–325 g on arrival. The rats were individually housed in a climate controlled colony room that was illuminated from 7:00 am to 7:00 pm. After one week of ad libitum access to food and water, they were placed on food restriction and maintained at 85% of their ad libitum weights throughout the experiment.

Apparatus The behavioral training apparatus consisted of eight individual chambers (20.5 × 22.0 × 22.5 cm) with stainless steel front and back walls, clear acrylic sides, and a floor made of 0.48-cm stainless steel rods spaced 1.9 cm apart. An illuminated clear acrylic food cup was recessed in a 5.0 × 5.0 cm opening in the front wall, and photocells at the front of the food cup recorded entries and time spent in the cup. Sucrose pellets (45 mg, Formula 5TUT, Test Diets, Richmond, IN) were delivered to the food cups by pellet feeders (Coulbourn H14-22; Allentown, PA). Locally fabricated retractable levers, which were operated quietly by pneumatic controls, were located 2.5 cm to the left and right of the food cup, 4.5 cm above the floor. Each lever was 3.2 cm wide, and protruded 2 cm into the chamber when extended through a 3.8 × 0.5 cm slot. Each chamber was enclosed inside a sound attenuating shell. An infrared light was located outside of each chamber, and cameras mounted within the shell allowed for television viewing and behavioral scoring.

Training procedures Table 1 provides an outline of the procedures of Experiment 1. Rats were first trained to eat from the food cups in a single 64-min session in which they received 16 deliveries of two sucrose pellets over a 1-s period, the event used as the reinforcer throughout this experiment. Next, the rats received ten 64-min sessions of discriminative autoshaping training in which 25 10-s extensions of one lever (L1+) were reinforced with two sucrose pellets, and 25 10-s extensions of the other lever (L2–) were not reinforced. For half the rats, left lever presentations were reinforced and for the other half, right lever extensions were reinforced. The trials were randomly intermixed in each session, with ITIs that averaged 77 s.

Next, the rats received four 64-min Phase 2 compound training sessions. In each session, the rats received 25 reinforced

Table 1 Outlines of procedures of Experiments 1–4

Experiment 1				
Group	Phase 1	Phase 2	Test	
BLK	L1+, L2–	L1N+	N?	
OVR	L1+, L2–	L2N+	N?	
Experiment 2				
Group	Phase 1	Phase 2	Test Auditory	Test Levers
BLK/OVR	L1+, L2–	L1A1+, L2A2+	A1–, A2–	L1–, L2–
CTL	L1+, L2–	A1+, A2+	A1–, A2–	L1–, L2–
Experiment 3				
Group	Phase 1	Phase 2	Test Levers	Test Auditory
BLK/OVR	A1+, A2–	A1L1+, A2L2+	L1–, L2–	A1–, A2–
CTL	A1+, A2–	L1+, L2+	L1–, L2–	A1–, A2–
Experiment 4				
Group	Phase 1	Phase 2	Test	
BLK	L1+, N–	L1L2+	L2–, L1–	
OVR	L1–, N+	L1L2+	L2–, L1–	
CTL/BLK	L1+, N–	L2+	L2–, L1–	
CTL/OVR	L1–, N+	L2+	L2–, L1–	

Tests of responding to the stimuli introduced during Phase 2 of each experiment were interspersed with Phase 2 training sessions. See the text for details. In Experiments 2 and 3, the identities (clicker or white noise) of the two auditory stimuli (A1 and A2) were completely counterbalanced, as were the locations (left or right) of the two levers (L1 and L2) in all experiments. BLK = blocking, OVR = overshadowing, CTL = control, N = white noise, + = food-reinforced, – = nonreinforced

presentations of a 10-s compound stimulus that comprised a 78-dB white noise and extension of either the previously reinforced lever (Group BLK) or the previously nonreinforced lever (Group OVR), counterbalanced by lever position (left or right). Mean ITIs were 154 s. Test sessions of responding to the added noise stimulus were given the day after Compound Training Sessions 2 and 4. Each of these tests was 20 min in duration and included eight nonreinforced presentations of the noise CS.

Automated response measures We reported the percentage of time rats spent with their heads in the food cup (goal-tracking) and the rate of lever pressing (sign tracking). Although in previous experiments (Chang et al., 2012b) we found that the percentage of trials on which at least one lever press occurred was affected differently by some brain lesions than the rate of lever pressing, throughout the present four experiments analyses of those two measures gave identical patterns of statistical significance, so we elected to present only the rate measure of sign tracking. Because the levels of both the sign- and goal-tracking responses peak during the last 5 s of 10-s lever presentations (Chang et al., 2012a, 2012b), as do goal-tracking responses to auditory cues (e.g., Holland, 2000), we presented the results of analyses of responding during that last 5-s period as our primary measures. The conclusions drawn from analyses confined to the first 5-s period and those from analyses for entire CS period were identical throughout all four experiments. Finally, we reported food cup behavior as elevation scores (responding during stimulus presentations minus responding during equivalent pre-CS periods). Because the interpretation of elevation scores between groups depends on comparable baseline scores, we also reported the pre-CS food cup behavior. Lever pressing was not possible prior to lever stimulus presentations, so lever press rates were not presented as elevation scores.

Behavioral observations For the test sessions that included auditory stimuli in Experiments 1 and 2, we scored several behaviors from videotapes, primarily to evaluate possible competition of responses directed to the lever sites with food cup entries. On each test trial, each rat's behavior was observed at 1.25-s intervals for 25 s, beginning 5 s before CS presentations. All observations were paced by auditory signals recorded on the videotapes. At each observation, one and only one behavior was recorded. Four behavioral categories were reported: food cup behavior, whenever the rat's head was in the recessed cup; reinforced (L1) or nonreinforced (L2) lever-site-directed behavior, whenever the rat's nose or paws was near the narrow opening through which the lever was normally extended, or between that opening and the food cup; and head jerk outside the food cup, short, rapid horizontal and/or vertical movements of the head when the rat's nose was not in the food cup. Head jerk behavior that occurred while the rat was in the food cup was scored as food cup behavior in these experiments. For each 5-s recording interval (5-s pre-CS, two 5-s during CS, and two 5-s post-CS intervals) considered separately, the numbers of each behavior scored were summed across each four-trial test block, and then multiplied by 100

and divided by the total number of observations made in that recording interval over the test block, to form the measure "% observed behavior." Because the number of observations made in each interval was constant, these measures were absolute, rather than relative, response measures.

Data analysis Initial analyses of variance (ANOVAs) that included the lever counterbalancing (left/right) variable showed no significant main effects or interactions (ps >.27) in any phase of the experiment, so that variable was excluded from our final ANOVAs. Thus, in Experiment 1, each measure was subjected to a mixed ANOVA with the between-subjects variable of group (BLK or OVR), and the within-subjects variables of contingency (reinforced or nonreinforced, if applicable), and sessions (or trial blocks).

Results

Two rats, one in each group, failed to press the reinforced lever, and instead spent 60%–70% of the time during reinforced lever presentations with their heads in the food cup. We identified these rats as "goal-trackers" (Flagel et al., 2009). Because the focus of our study was autoshaped lever pressing and we found only three goal-trackers among the 68 rats used in the present series of experiments, we excluded from analysis all data from these goal-trackers.

The left portions of Fig. 1 show the results of the discriminative autoshaping training phase. Figure 1a shows the rate of lever pressing. On average, the rats acquired the discrimination rapidly, but there was substantial variation across subjects. Unfortunately, although rats were assigned randomly to the two groups prior to beginning the experimental procedures, the patterns of acquisition over sessions differed between the two groups, which were treated identically in this phase. However, the groups attained similar levels of responding by the last five sessions. ANOVAs showed significant effects of contingency [$F(1, 12) = 55.32$, $p < .001$] and session [$F(9, 108) = 11.81$, $p < .001$] and a Contingency × Session interaction [$F(9, 108) = 19.38$, $p < .001$]. Although the main effect of group was not significant ($p = .711$), the Group × Contingency × Session interaction was [$F(9, 108) = 4.27$, $p < .001$]. Over the last five sessions only, effects involving the group variable were not significant (ps > .400).

Figure 1b shows elevations in the percentage of time in the food cup during lever presentations. Although most rats acquired food cup responding early in training, that responding waned as lever pressing became more frequent. As with lever pressing, the identically treated groups appeared to differ, but these differences were not significant. The only significant effects were those of contingency [$F(1, 12) = 12.16$, $p = .004$] and session [$F(9, 108) = 8.04$, $p < .001$] and their interaction [$F(9, 108) = 8.49$, $p < .001$]; none of the effects involving group

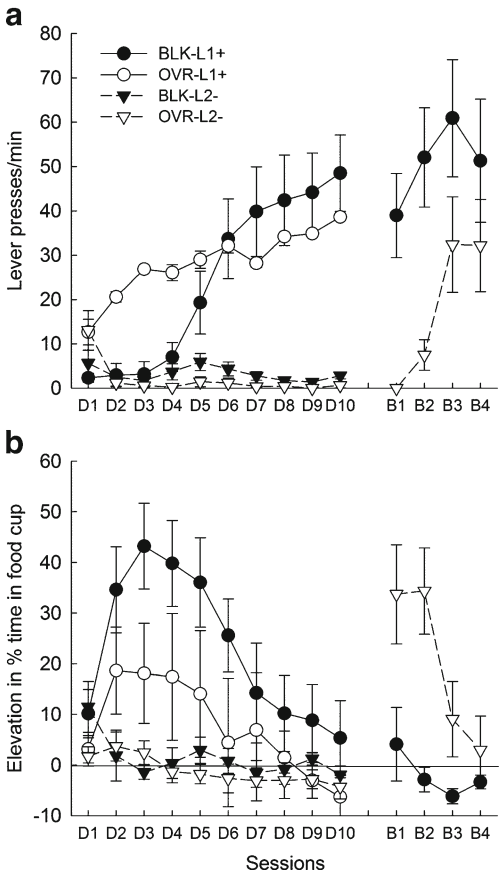

Fig. 1 Lever-press (**a**) and food cup (**b**) responding during the Phase 1 discrimination training (D sessions) and Phase 2 compound training (blocking; B sessions) of Experiment 1. BLK = blocking group, OVR = overshadowing control group, L1+ = food-reinforced lever, L2– = nonreinforced lever. Food cup responding is expressed as the elevation of responding during cue presentations over baseline responding. All entries are means ± *SEM*s

were reliable (ps >.140). An ANOVA of pre-CS food cup responding (which declined steadily from 16.6% ± 2.2% in Session 1 to 7.0% ± 2.4% in Session 10) showed a significant effect of session [$F(9, 108) = 5.58$, $p < .001$] and a significant Group × Session interaction [$F(9, 108) = 5.36$, $p < .001$], such that pre-CS responding was initially greater in Group BLK than in Group OVR (12.2% ± 2.8% vs. 9.0% ± 2.1% over Sessions 1–5), but later in training was greater in Group OVR (10.0% ± 4.1% vs. 4.7% ±1.4% over Sessions 6–10).

In Phase 2 compound training, the behavior of rats in Groups BLK and OVR during the noise + lever compound differed substantially (right portions of Fig. 1). Rats in Group BLK maintained high levels of lever pressing and low levels of food cup behavior in the presence of the compound of the noise and the previously reinforced lever, whereas rats in Group OVR initially acquired moderate levels of food cup behavior, which decreased over sessions, as lever pressing to the previously nonreinforced lever was acquired. An ANOVA of lever-press rates (Fig. 1a) showed significant effects of group [$F(1, 12) = 6.35$, $p = .027$] and session [$F(3, 36) =$

12.61, $p < .001$] and their interaction [$F(3, 36) = 2.78$, $p = .050$]. Tests of simple effects of group for each session showed significant differences in each of the first two sessions (ps < .003). An ANOVA of the elevation in food cup responding (Fig. 1b) also showed significant effects of group [$F(1, 12) = 13.68$, $p = .003$] and session [$F(3, 36) = 6.05$, $p = .002$], as well as their interaction [$F(3, 36) = 3.08$, $p = .040$]. Tests of the group effect showed significant differences on the first two sessions only (ps < .032). An ANOVA of pre-CS food cup responding (which ranged from 10.2% ± 3.0% in Session 1 to 6.1% ± 2.4% on Session 4) showed no effect or interaction involving group (ps > .503) and only a marginally significant effect of sessions ($p = .075$).

Figure 2 shows the results of the tests of responding to the added noise cue. The first test occurred after the first two compound training sessions, and the second test occurred after the last two training sessions. Figure 2a shows elevation in food cup responding during the last 5-s interval of the noise CS for each four-trial block of testing. The rats in Group BLK displayed less food cup responding to the added noise cue than did the rats in Group OVR in the first block of four trials in the first test. Thus, blocking of conditioning to the noise was observed. Indeed, this blocking was complete, as the elevation scores were not significantly greater than zero ($p = .105$). However, responding to the noise in Group OVR extinguished rapidly in the first test, as is indicated by reduced responding in the second block of trials in that test. Moreover, despite two additional noise + lever compound training sessions, neither group responded to the noise in the second test. These trends were especially evident in the last 5-s interval during the CS and in the first 5-s empty interval after noise presentation (when food would normally have been available); Fig. 2b shows responding in the first test block during the 5-s pre-CS period, each of the two 5-s noise periods, and each of two 5-s postnoise periods.

A Group × Test Period × Session Block ANOVA of absolute levels of food cup responding showed a significant interaction of group and test period [$F(4, 48) = 3.13$, $p = .0230$]. Furthermore, Group × Session Block ANOVAs of elevation scores for the last 5 s of the noise, and of elevation scores that included that interval as well as the subsequent 5- or 10-s empty intervals, all showed significant effects of group [Fs(1, 12) > 5.05, ps < .044]. The simple effects of group were significant only for the first block of test trials ($p = .022$; other ps > .254). An ANOVA of pre-CS food cup responding (7.2% ± 2.9% in Group BLK and 11.3% ± 4.5% in Group OVR) showed no significant effects or interaction (ps > .215).

Behavioral observations from videotapes indicated that the test results were not contaminated by competition from responses directed toward the sites of the absent levers. First, we observed relatively low levels of such responses in any of the observation intervals (pre-, during-, and post-CS), in any of the four test blocks. As with the automated food cup measure

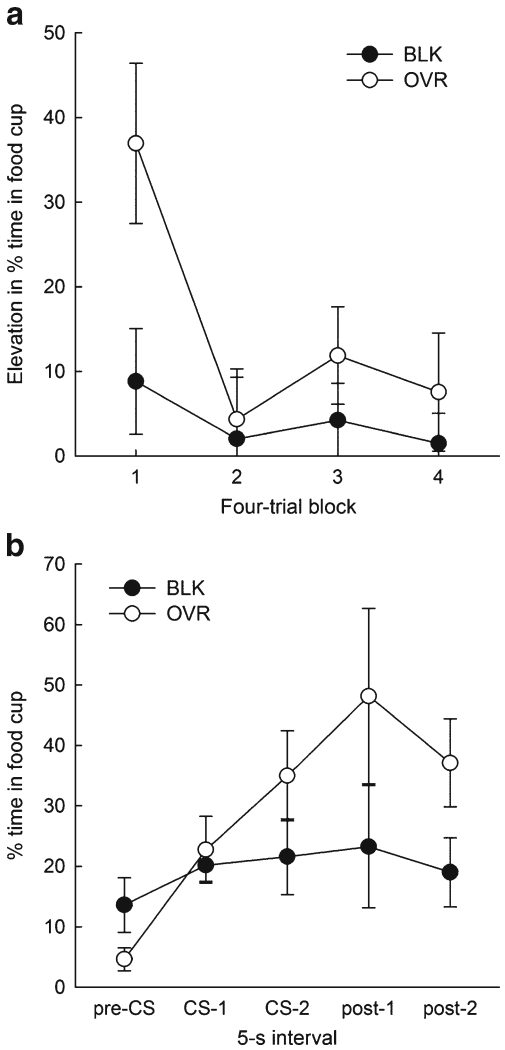

Fig. 2 Food cup responding in the test sessions of Experiment 1. Panel **a** shows the elevation over baseline responding of responding during the last 5-s interval of the noise conditioned stimulus (CS) for each four-trial block of testing. Two sessions of Phase 2 compound training occurred between the second and third test blocks. Panel **b** shows responding in the first test block, during the 5-s pre-CS period, each of the two 5-s CS periods, and each of the two 5-s post-CS periods. BLK = blocking, OVR = overshadowing. All entries are means ± *SEM*s

(Fig. 2b), the highest levels of responding were observed during the last 5-s observation interval during the CS and the first 5-s post-CS interval. Thus, we constructed elevation scores by subtracting pre-CS responding from responding averaged across those two intervals. These elevation scores ranged from −0.9% ± 3.5% to 5.8% ± 2.9% of observations for behaviors directed toward the site of the lever that was reinforced in discrimination training (L1), and from −2.7% ± 4.0% to 4.5% ± 1.5% for the site of the lever that was previously nonreinforced (L2). Pre-CS responding ranged from 0.9% ± 0.9% to 8.0% ± 3.5%. Group × Test Block ANOVAs for these measures showed no significant main effects or interactions [Fs < 1.89, ps > .149]. Second, head-jerk behaviors occurring outside of the food cup were also

uncommon, occurring on less than 10% of observations in the first test bock and less than 2.7% thereafter; this behavior did not occur during pre-CS intervals. An ANOVA for this measure showed a main effect of block [$F(3, 36) = 6.83$, $p < .001$] but neither the effect of group [$F(1, 12) = 3.03$, $p = .107$] nor the Group × Block interaction [$F(3, 36) = 1.39$, $p = .261$] was significant. Third, observations of food cup behavior were very similar to, and strongly correlated with, the automated measure reported previously (Fig. 2a). On the first test block, the observed food cup elevation scores were 43.8% ± 8.9% in Group OVR and 8.5% ± 4.0% in Group BLK. A Group × Block ANOVA showed significant effects of group [$F(1, 12) = 14.21$, $p = .003$] and blocks [$F(3, 36) = 5.23$, $p = .004$], and the overall correlation between video and automated measures of elevation in time in the food cup was $r = .91$ ($p < .001$). Finally, the correlation between food cup and reinforced lever-site-directed elevation scores overall ($r = +.55$) was significant (two-tailed $p = .041$), with the maximum correlation on the first block of the second test session ($r = .71$, two-tailed $p = .005$). No other correlations among behaviors were significant (rs < .36, ps > .220).

Discussion

We found no evidence for conditioning of the noise in Group BLK. Thus, prior conditioning of the lever completely blocked conditioning to the noise when a noise + lever compound was paired with food in the second phase. Furthermore, although the noise acquired considerable food cup responding over the first two compound training sessions in Group OVR, allowing the claim that blocking occurred, that responding was lost over the subsequent two compound training sessions, as the previously nonreinforced lever acquired conditioning. Although Experiment 1 had no noise-alone control for overshadowing, from other experiments in this laboratory we would expect elevation scores close to 50% after four training sessions with noise alone. Experiment 2 provided such a control.

The pattern of data observed in the test sessions was foreshadowed in the compound training itself. Although food cup responding was never acquired in that phase in Group BLK, substantial levels occurred during the first two compound sessions in Group OVR, only to decline over the subsequent sessions. This decline may have reflected loss of conditioning to the noise, or simply competition from the lever press responses that were being acquired to the previously nonreinforced lever (Costa & Boakes, 2009). However, if competition from lever pressing were responsible, one would have expected food cup responding to be revealed in tests of the noise alone, which was not the case. Furthermore, observation of behaviors directed toward the lever sites in the test sessions (in which the levers themselves were absent) showed little evidence for such competition. Indeed, we observed a positive correlation between the frequency of food cup and lever-site responses, rather than the negative correlation one would expect if the two responses competed. Finally, some of the failure to observe responding in the noise-alone tests might be attributed to within-test extinction of that responding. This possibility was addressed in Experiment 2.

Experiment 2

Experiment 2 examined blocking of conditioning to an auditory cue by a previously conditioned lever CS using a within-subjects design. All rats first received discrimination training in which one lever was reinforced and another nonreinforced. Then, each rat in Group BLK/OVR received reinforced presentations of two lever + auditory cue compounds. The BLK compound comprised an auditory cue and the previously reinforced lever, and the OVR compound comprised another auditory cue and the previously nonreinforced lever. Each rat in Group CTL received conditioning of the two auditory cues alone in this phase. Finally, responding to the auditory cues alone was examined. Blocking would be indicated by greater responding to the auditory cue from the OVR compound than to the auditory cue from the BLK compound in Group BLK/OVR. Overshadowing would be indicated by greater responding to the auditory cues alone in Group CTL than to the OVR cue in Group BLK/OVR.

Method

Subjects and apparatus The subjects were 12 naïve male Long-Evans rats, obtained and maintained as those of Experiment 1. The apparatus comprised six of the chambers used in Experiment 1.

Procedures Table 1 shows an outline of the procedures of Experiment 2. After a single food cup training session, as in Experiment 1, all rats received 16 10-s lever insertions (L1+) reinforced with the delivery of two sucrose pellets, in each of two 64-min sessions. For half of the rats, the reinforced lever was the right lever and for the other half it was the left lever. Next, the rats received six 64-min lever discrimination training sessions, each including eight reinforced 10-s insertions of the lever presented in the previous sessions, interspersed randomly with eight nonreinforced 10-s insertions of the other lever (L2–).

The rats in Group BLK/OVR ($n = 6$) then received six 64-min Phase 2 training sessions with two 10-s compounds of auditory and lever-insertion stimuli. The BLK compound comprised A1 (either an 80-dB white noise or an 80-dB 6-Hz clicker, counterbalanced) combined with insertion of the previously reinforced lever (L1), and the OVR compound comprised the other auditory stimulus (A2) combined with

insertion of the previously nonreinforced lever (L2). One would thus expect that conditioning to the auditory cue in the BLK compound (A1) would be blocked relative to conditioning to the auditory cue in the OVR compound (A2). Rats in Group CTL (n = 6) received conditioning of A1 and A2 alone in the absence of any levers in this phase, to permit evaluation of effects of overshadowing of conditioning to the auditory cues by the presence of the previously nonreinforced lever in the OVR compound in Group BLK/OVR. The identities of the auditory and lever stimuli, and their combinations, were counterbalanced for each compound in Group BLK/OVR. Although Group CTL received no compounds, the roles of noise and clicker as "blocking" (BLK) and "overshadowing" (OVR) control stimuli were assigned in mock counterbalancing conditions to facilitate data analysis.

As in Experiment 1, conditioned responding to the auditory stimuli was evaluated in nonreinforced test sessions after each pair of Phase 2 training sessions. The first of these sessions was 32-min in duration, and included four 10-s noise and four 10-s clicker presentations in a balanced order. The next two sessions were each 64 min in duration. The first 32 min of each of these tests included four 10-s noise and four 10-s clicker presentations (identical to Test 1 except for trial order). The remaining 32 min included the insertion each of the two levers was inserted four times for 10-s periods, also in a balanced order. No reinforcers were presented in any of these sessions. We scored lever-site-directed behaviors, as in Experiment 1, during tests of the auditory stimuli in the first and third test sessions.

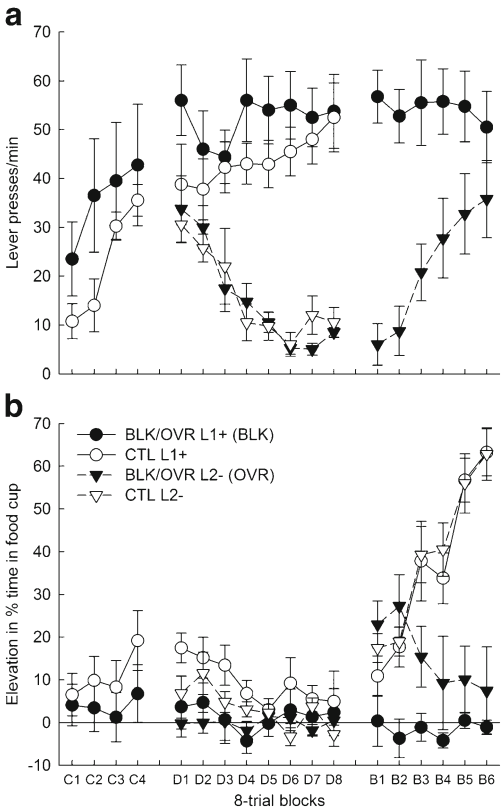

Fig. 3 Lever-press (**a**) and food cup (**b**) responding during Phase 1 nondiscriminative (**c** sessions) and discrimination (D sessions) training and during Phase 2 (blocking; B sessions) training of Experiment 2. BLK/OVR = blocking/overshadowing group, CTL = control group, L1+ = food-reinforced lever, L2– = nonreinforced lever. In Group BLK/OVR, L1+ served as the blocking stimulus and L2– served as the overshadowing stimulus. Food cup responding is expressed as the elevation of responding during cue presentations over baseline responding. All entries are means ± *SEM*s

Results

All 12 rats were identified as "sign-trackers" and were included in the analyses. The left panels of Fig. 3 show the results of the initial and discriminative autoshaping training phases. Figure 3a shows the rates of lever pressing. Initial ANOVAs that included the lever counterbalancing variable showed no effects or interactions of that variable (ps > .410), so it was eliminated from the subsequent analyses. A Group × Session ANOVA of responding during the four 8-trial blocks of nondiscriminative training showed a significant effect of sessions [$F(3, 30) = 9.16$, $p < .001$] but no significant effect of group or Group × Session interaction (ps > .236). A Group × Contingency × Session ANOVA over discrimination training showed significant effects of contingency [$F(1, 10) = 70.11$, $p < .001$], session [$F(7, 70) = 4.56$, $p < .001$], and the Contingency × Session interaction [$F(7, 70) = 12.30$, $p < .001$]. Neither the main effects of group (ps > .239) nor any of its interactions (ps > .290) was significant.

Figure 3b shows the elevation in percentages of time in the food cup during lever presentations. Unlike in Experiment 1, little evidence for discriminative food cup responding during lever insertions is apparent. An ANOVA of elevation scores showed only a significant effect of sessions [$F(7, 70) = 3.76$, $p = .002$] and a significant Group × Session interaction [$F(7, 70) = 2.58$, $p = .020$]: Group CTL showed higher elevation scores over the first half of training, but not the last half. We found no effects of contingency ($p = .111$) or its interactions (ps > .314). An ANOVA of pre-CS food cup responding (4.9% ± 2.4% in Group BLK and 3.5% ± 2.0% in Group OVR) showed no significant main effects or interactions (ps > .177).

The right portions of Fig. 3 show performance during Phase 2 training. In Group BLK/OVR, pressing of the previously reinforced lever (L1+) was maintained despite the addition of an auditory cue, and pressing of the previously nonreinforced lever (L2–) was rapidly acquired. In Group BLK/OVR, no evidence emerged for acquisition of food cup behavior to the "BLK" compound (which included L1+), whereas moderate amounts were acquired to the "OVR" compound (which included L2–). Notably, as in Experiment 1, although food cup responding to the OVR compound was acquired in the early Phase 2 training sessions, it declined as

that training continued. By contrast, in Group CTL food cup responding to the auditory stimuli continued to increase throughout Phase 2.

Initial ANOVAs that included the counterbalancing variables of lever and auditory cue identity (left/right and clicker/noise) showed no significant main effects or interactions for those variables (ps > .111), so they were omitted from subsequent ANOVAs. A Compound Type (BLK vs. OVR) × Session ANOVA of lever-press rate in Group BLK/OVR (the only group that received levers in this phase) showed significant effects of compound [$F(1, 5) = 35.43$, $p = .002$], session [$F(5, 25) = 5.76$, $p < .001$], and their interaction [$F(5, 25) = 3.72$, $p = .012$]. The simple effects of group were significant (ps < .050) for each session. A Compound × Session ANOVA of food cup elevation scores showed significant main effects of group [$F(1, 10) = 33.68$, $p < .001$], compound [$F(1, 10) = 5.29$, $p = .044$], and session [$F(5, 50) = 9.94$, $p < .001$] and significant interactions of both group [$F(5, 50) = 19.64$, $p < .001$] and compound [$F(5, 50) = 2.95$, $p = .021$] with session. Within Group BLK/OVR, food cup elevation scores were initially higher during the OVR compound than during the BLK compound, but that difference declined over sessions (linear trend $p = .020$). The BLK versus OVR difference was significant for Sessions 1, 2, and 3 (ps < .020) but not Sessions 4, 5, or 6 (ps > .126). An ANOVA of pre-CS food cup responding (3.9% ± 1.9% in Group BLK/OVR and 5.8% ± 2.2% in Group CTL) showed no significant effects or interactions (ps > .107).

Figure 4a shows the results of the tests of responding to the added auditory cues, which occurred after Phase 2 Training Sessions 2, 4, and 6. The rats in Group BLK/OVR showed greater food cup responding to the auditory cue that was included in the OVR compound (A2) than to the auditory cue that had been part of the BLK compound (A1). Thus, blocking occurred. However, as in Experiment 1, food cup responding to the OVR auditory cue declined with more training of the OVR compound, and no evidence emerged for greater responding to the OVR auditory cue than to the BLK auditory cue in Test 3, after six Phase 2 training sessions. By contrast, in Group CTL, food cup responding to the auditory cues increased over the course of Phase 2 training and testing. A Group × Cue × Test Session ANOVA of elevation scores showed significant effects of group [$F(1, 10) = 21.15$, $p < .001$] and session [$F(2, 20) = 4.71$, $p = .021$] and a Group × Session interaction [$F(2, 20) = 4.76$, $p = .020$]. Post-hoc Tukey HSD tests indicated that the BLK cue (A1) showed greater responding in Group CTL than in Group BLK/OVR in both Tests 2 and 3 (ps < .015) and the OVR cue (A2) showed greater responding in Group CTL in the final test session ($p = .016$). This last difference demonstrates overshadowing of conditioning of the auditory cue. Finally, an ANOVA of pre-CS food cup responding showed no significant effects [$F(1, 10) < 2.14$, ps > .175].

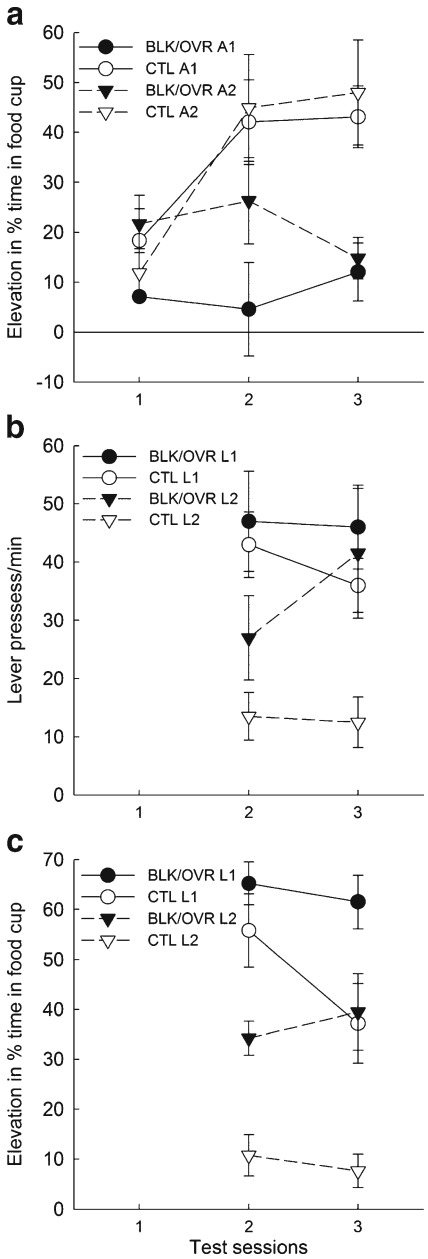

Fig. 4 Responding during the test sessions of Experiment 2. Panel **a** shows food cup responding during tests of responding to the added auditory stimuli. The points labeled A1 and A2 refer to responding to the blocked and overshadowed cues, respectively, in Group BLK/OVR (blocking/overshadowing), or to responding to separately trained auditory cues in Group CTL (control) with counterbalancing identities comparable to those in Group BLK/OVR. Two Phase 2 training sessions occurred before each of the three test sessions. Panel **b** shows lever-press responding during the tests of responding to the levers, which occurred immediately after the second and third tests of responding to the auditory cues (see the text for details). Panel **c** shows food cup responding during the 5-s period after withdrawal of the levers (relative to pre-lever-insertion baseline responding) in the tests shown in panel **b**. In panels **b** and **c**, the points labeled L1 and L2 refer to responding to levers that had been reinforced or nonreinforced, respectively, in the discrimination training phase. All entries are means ± *SEM*s

As in Experiment 1, behavioral observations from videotapes suggested that the test results were not importantly affected by competition from responses directed toward the sites of the absent levers. We observed relatively low levels of such responses in each of the tests, with elevation scores no greater than 6.8% ± 1.7% for any stimulus/group combination. A Group (BLK/OVR or CTL) × Response (L1 or L2) × Stimulus (BLK or OVR) ANOVA showed only a marginally significant effect of test, with elevation scores declining from 4.2% ± 2.5% in the first test to 1.2% ± 2.2% in the third test [$F(1, 10) = 4.71$, $p = .055$, other ps > .129]. Thus, differences in food cup responding could not be systematically related to differences in lever-site-directed responses.

Figures 4b and c show the results of the two tests of responding to the lever stimuli, which were administered immediately after the second and third tests of responding to the auditory cues. Consistent with the training conditions, in Group CTL, lever pressing to the previously nonreinforced lever (L2–) occurred at low levels, and lever pressing to the previously reinforced lever (L1+) occurred at high levels, with a slight decline in the latter responding over the course of the two nonreinforced test sessions. Similarly, in Group BLK/OVR, lever pressing was rapidly acquired to L2– when it was reinforced in compound with a novel auditory cue (OVR compound), and responding remained high to L1+, which continued to be reinforced in the BLK compound. We found little evidence for food cup behavior during lever presentations in any condition (<5% elevation; not shown). However, during the 5-s interval after the lever was withdrawn (and when food would have been delivered), food cup behavior (Fig. 4c) showed patterns similar to that of lever-press responding.

A Group × Cue × Session ANOVA of lever-press rates showed significant effects of group [$F(1, 10) = 4.66$, $p = .050$] and cue [$F(1, 10) = 10.69$, $p = .008$]. Post-hoc Tukey HSD tests showed that responding to L2– in Group CTL was lower than responding in any of the other conditions in the third test session (ps < .01); in the second test session, it was lower than that to the reinforced levers in either group (ps < .01), but did not differ significantly from responding to L2– in Group BLK/OVR ($p > .05$). Finally, a Group × Cue × Session ANOVA of food cup elevation scores during the first 5-s postlever interval showed a pattern similar to that shown for lever pressing, with significant effects of group [$F(1, 10) = 23.27$, $p < .001$] and cue [$F(1, 10) = 38.69$, $p < .001$].

Discussion

The results of Experiment 2 replicated all aspects of the results of Experiment 1. First, once again, conditioning of an auditory cue was completely blocked by prior conditioning of a lever cue. Second, although conditioned food cup responding to an auditory cue alone was initially acquired in the overshadowing condition (BLK/OVR), that responding declined with further lever + auditory cue training, as the lever acquired more conditioned responding. That loss was not readily accountable in terms of competition from lever-site-directed responses during the auditory cue tests because those latter responses occurred at low levels and also declined as compound conditioning proceeded. Thus, not only did the previously nonreinforced lever overshadow new learning about an auditory cue, but it also appeared to take existing conditioning away from that cue. Third, the results of the noise-alone tests were presaged by the form and amount of responding observed during the compounds during Phase 2 training itself. Because conditioned responding to the lever cues was almost exclusively directed to the levers, and conditioned responding to the auditory cues was directed to the food cup, learning about the lever and noise could be independently observed in the presence of auditory + lever compounds. A similar point was made by Holland (1977), who examined blocking of conditioning across auditory and visual cues that controlled CRs of very different forms. Finally, going beyond the findings of Experiment 1, the high levels of responding to the auditory cues in the CTL condition showed that the low levels of responding to the noise in the BLK/OVR condition were due to overshadowing (i.e., the presence of a lever during Phase 2 compound training) rather than generally slow learning about the noise or loss of that responding in testing because of intra-test session extinction.

Our use of a discriminative conditioning procedure in Phase 1 in these experiments requires comment. Relative to procedures in which the effects of a previously reinforced CS+ are contrasted with the effects of a novel control stimulus, the discriminative conditioning procedure has several advantages. First, it better matches simple exposure to both blocking and control stimuli, which is relevant to learning theories in which novelty is a critical variable (Schmajuk, Lam, & Gray, 1996) or in which either nonreinforced or reinforced presentations of a stimulus can reduce its associability (e.g., Pearce & Hall, 1980). Second, it reduces generalization between the blocking and control stimuli, which could otherwise reduce the apparent magnitude of blocking, especially when those stimuli are drawn from the same modality, as in the present experiments.

However, it could be argued that the discriminative training procedure might establish conditioned inhibition to the nonreinforced CS– control cue. In that case, Phase 2 reinforcement of the added cue in compound with CS– might produce "superconditioning" of the added "overshadowed" cue (e.g., Pearce & Redhead, 1995). Hence, comparison of overshadowed and blocked cues in test might overestimate the magnitude of the blocking effect, and comparison of the overshadowing cue with a control cue that was separately trained might underestimate the magnitude of the overshadowing effect. Similarly, within some conditioning theories, nonreinforced exposure to CS– might cause rats to acquire latent inhibition to that cue, which could influence its ability to overshadow or block learning to the added

cues in Phase 2. Nevertheless, we believe that in the present experiments the advantages of the discriminative procedure outweighed its disadvantages. Although we have no independent assessments of conditioned or latent inhibition to CS–, CS– did not suppress baseline food cup responding nor reduce lever-press responding to zero, and acquisition of food cup or lever press responding to CS– in Phase 2 appeared at least as rapid as to CS+ in Phase 1, throughout these experiments. Furthermore, we used the same Phase 1 discriminative procedure in all four experiments in this series. Thus, it would be unlikely that any such contamination of our blocking and overshadowing effects would contribute to the substantial differences in outcomes we observed across these studies.

Experiment 3

Experiment 3 examined the ability of auditory cues to block or overshadow conditioning to lever-extension cues. Its design was identical to that of Experiment 2 except that the roles of auditory and lever-extension cues were reversed.

Method

Subjects and apparatus The subjects were 14 naïve male Long-Evans rats, obtained and maintained as those of Experiments 1 and 2. The apparatus was that used in Experiment 1.

Procedures Table 1 shows an outline of the procedures of Experiment 3. After a single food cup training session, all rats received 16 10-s presentations of an auditory cue (A1+, either the noise or clicker used in Exp. 2), reinforced with the delivery of two sucrose pellets, in each of two 64-min sessions. Next, the rats received six 64-min auditory discrimination training sessions, each including eight A1+ presentations, interspersed randomly with eight nonreinforced 10-s presentations of the other auditory cue (A2–).

The rats in Group BLK/OVR (n = 8) then received six 64-min Phase 2 training sessions with two 10-s compounds of auditory and lever-insertion stimuli. The BLK compound comprised L1 (left or right lever, counterbalanced) combined with the previously reinforced auditory cue (A1), and the OVR compound comprised the other lever (L2) combined with the previously nonreinforced auditory stimulus (A2–). One would thus expect that conditioning to L1 in the BLK compound would be blocked relative to conditioning to L2 in the OVR compound. In this phase, the rats in Group CTL (n = 6) received conditioning of each lever in the absence of any auditory stimuli, to permit evaluation of effects of overshadowing of conditioning to the lever cues by the presence of the previously nonreinforced auditory cue in the OVR compound in Group BLK/OVR. The identities of the auditory and lever stimuli, and their combination, were counterbalanced for each compound in Group BLK/OVR. Although Group CTL received no compounds, the roles of each lever as BLK (L1) and OVR (L2) control stimuli were assigned in mock counterbalancing conditions to facilitate data analysis.

Conditioned responding to the lever stimuli was evaluated in nonreinforced test sessions after each pair of Phase 2 conditioning sessions. The first of these sessions was 32-min in duration, and included four 10-s left lever and four 10-s right lever presentations in counterbalanced order. The next two sessions were identical to Test 1 (except for trial order) for the first 32 min, but then included an additional 32 min in which each of the two auditory stimuli was presented four times for 10-s periods, also in counterbalanced order. No reinforcers were presented in any of these sessions.

Results

The left and center portions of Fig. 5 show acquisition of food cup responding to the auditory cues over the course of the conditioning and discrimination training phases, respectively. Because initial analyses showed effects of the identity of the auditory cues during discrimination training, that variable was retained for all subsequent ANOVAs. A Group × Auditory Cue (clicker/noise) × Session ANOVA of elevation of food cup responding in the nondiscriminative training sessions showed a marginally significant effect of auditory cue identity [clicker > noise: $F(1, 10) = 4.17$, $p = .068$] and a significant

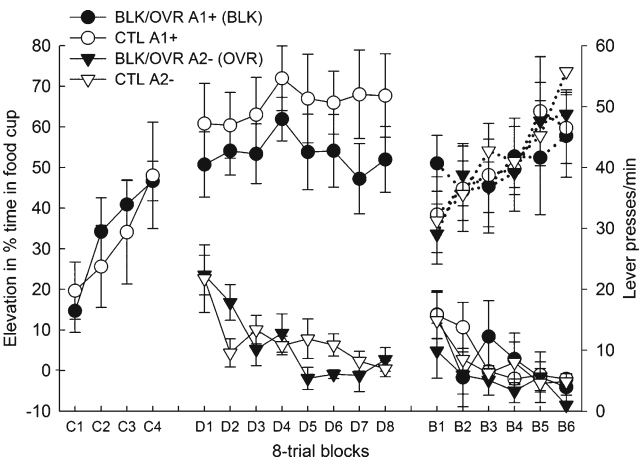

Fig. 5 Food cup responding during the Phase 1 nondiscriminative (C sessions) and discrimination (D sessions) training, and during Phase 2 (blocking; B sessions) training of Experiment 3. BLK/OVR = blocking/overshadowing group, CTL = control group, A1+ = food-reinforced auditory cue, A2– = nonreinforced auditory cue. In Group BLK/OVR, A1+ served as the blocking stimulus and A2– served as the overshadowing stimulus. Food cup responding (left ordinate scale) is expressed as the elevation of responding during cue presentations over baseline responding. Lever-press rates (right scale; dotted lines) to L1 (circles) and L2 (inverted triangles) are shown for the compound training (when levers were first introduced). All entries are means ± *SEM*s.

effect of session [$F(3, 30) = 9.48$, $p < .001$]. None of the interactions involving auditory cue identity was significant (ps > .151). An ANOVA of pre-CS food cup behavior, which averaged 10.7% ± 3.6% in Group BLK and 8.1% ± 3.1% in Group CTL, showed no significant effects or interactions (ps > .163). A Group × Auditory Cue × Contingency × Session ANOVA of food cup elevation scores in the discrimination training phase showed a significant effects of auditory cue [clicker > noise, $F(1, 10) = 4.96$, $p = .050$] and contingency [$F(1, 10) = 130.23$, $p < .001$], and significant interactions of both Contingency × Session [$F(7, 70) = 6.50$, $p < .001$] and Contingency × Auditory Cue Identity [the discrimination was better when the clicker was the reinforced cue: $F(1, 10) = 5.09$, $p = .048$]. No other interactions of auditory cue identity approached significance (ps > .244). An ANOVA of pre-CS responding, which averaged 6.4% ± 2.8% in Group BLK and 3.0% ± 1.4% in Group CTL, showed marginally significant effects of group [$F(1, 12) = 4.01$, $p = .068$] and Group × Session interaction [$F(7, 84) = 1.91$, $p = .078$].

The right portions of Fig. 5 show responding to the stimuli in Phase 2. All rats rapidly acquired lever pressing to both compound cues in Group BLK/OVR or to both individual levers in Group CTL (right scale in Fig. 5). Initial ANOVAs showed no significant effects or interactions with lever identity (left/right), so that variable was omitted from the subsequent ANOVAs. A Group × Auditory Cue Identity × Cue (BLK vs. OVR) × Session ANOVA for lever-press rates showed a main effect of session [$F(5, 50) = 5.29$, $p < .001$], greater responding in the presence of the clicker than in the presence of the noise [$F(1, 10) = 7.99$, $p = .018$], and decreasing differences between responding during clicker and noise stimuli as the phase proceeded [Cue Identity × Session interaction: $F(5, 50) = 3.12$, $p = .016$]. A comparable ANOVA of food cup elevation scores (left scale) showed only a significant effect of session [$F(5, 50) = 8.07$, $p < .001$], and an ANOVA of pre-CS food cup scores showed no significant effects or interactions (ps > .404).

Figure 6 shows the results of the test sessions. Evidence for blocking or overshadowing of lever-press acquisition by a previously trained auditory cue was minimal at best. A Group × Auditory Cue Identity × Lever Treatment (BLK vs. OVR) × Session ANOVA of lever-press rates (Fig. 6a) showed only a significant effect of session [$F(2, 20) = 5.21$, $p = .015$] and an auditory Cue Identity × Lever Treatment interaction [$F(1, 10) = 6.92$, $p = .025$], indicating greater responding to the BLK lever if it had been trained in compound with the initially more-conditioned clicker cue than with the noise. Despite this lack of overall evidence for blocking or overshadowing, we explored the lever-press data further for any suggestion of these phenomena. Consider first the primary, within-subjects comparison for blocking. In the first test, the rats in Group BLK/OVR showed a higher rate of responding to the BLK lever (L1), which was being conditioned in the presence of a previously trained auditory cue, than to the OVR lever [$F(1, 12) =$

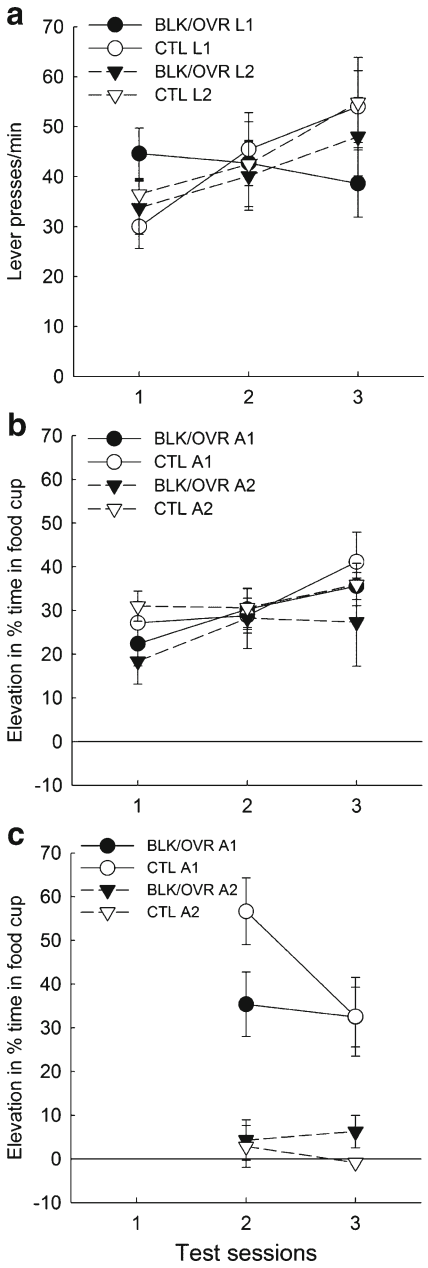

Fig. 6 Responding during the test sessions of Experiment 3. Panel **a** shows lever-press responding during tests of responding to the added lever stimuli. The points labeled L1 and L2 refer to responding to the blocked and overshadowed levers, respectively, in Group BLK/OVR (blocking/overshadowing), or to responding to separately trained levers in Group CTL (control), with counterbalancing identities comparable to those in Group BLK/OVR. Two Phase 2 training sessions occurred before each of the three test sessions. Panel **b** shows food cup responding during the 5-s period after withdrawal of the levers (relative to pre-lever-insertion baseline responding) in the tests shown in Panel **a**. Panel **c** shows food cup responding during the tests of responding to the auditory cues, which occurred immediately after the second and third tests of responding to the levers (see the text for details). In panel **c**, the points labeled A1 and A2 refer to responding to auditory cues that had been reinforced or nonreinforced, respectively, in the discrimination training phase. Entries in panel **c** represent elevation over baseline responding. All entries are means ± *SEM*s

7.59, $p = .020$]. This outcome is the opposite of what would be expected if prior reinforced training of the auditory cue blocked conditioning to the added lever. Over the course of the six Phase 2 compound training sessions (i.e., across the three test sessions), although additional responding was acquired to the OVR lever (L2), which was being trained in compound with the previously nonreinforced auditory cue, no such increase was observed to the BLK lever (L1). Although this difference in (linear) trends over test sessions was significant [$F(1, 12) = 9.68$, $p = .011$], even on the final test session, responding to L1 was only marginally lower than responding to L2 [$F(1, 12) = 4.54$, $p = .059$]. Thus, the evidence for blocking of lever pressing by previously reinforced auditory cues was unconvincing.

Overshadowing was evaluated by comparing responding to the OVR lever (L2) between Group BLK/OVR, in which that lever had been trained in compound with a previously nonreinforced auditory cue (A2), and Group CTL, in which that lever had been trained by itself. No differences in the rates of responding, either in the trend across sessions or in any individual session, were significant (ps > .710). Thus, the presence of an auditory stimulus did not appear to overshadow new learning to a lever stimulus.

We also considered the possibility that the auditory cues might have blocked or overshadowed acquisition of food cup behavior controlled by the levers. The rats showed little evidence for food cup behavior during lever presentations, in most cases showing some suppression in food cup behavior, as compared to their pre-CS responding. An ANOVA of these elevation scores yielded no significant effects or interactions (ps > .310). However, lever–food association was also indicated by the performance of food cup behavior after the levers were withdrawn, when the food would normally be delivered. Figure 6b shows elevation scores (relative to pre-CS levels) of food cup behavior for the 5-s period after lever withdrawal. An ANOVA of these scores also yielded no significant main effects or interactions (ps > .272), except for a marginal effect of session [$F(2, 10) = 3.37$, $p = .055$]. An ANOVA of pre-lever-extension food cup behavior (7.1% ± 2.9% in Group BLK/OVR and 2.8% ± 1.6% in Group CTL) showed no significant effects or interactions (lowest $p = .108$, for the effect of group). Thus, we found no evidence for blocking or overshadowing of conditioning of food cup responses to the levers by the auditory cues.

Figure 6c shows food cup elevation scores to the auditory stimuli during Test Sessions 2 and 3. Responding to the previously reinforced auditory cues was maintained at higher levels than was responding to the previously nonreinforced cues [$F(1, 10) = 85.07$, $p < .001$] in both groups [Group × Cue interaction: $F(1, 10) = 3.65$, $p = .085$]. That difference was especially large if the reinforced cue had been the clicker [Cue Identity × Cue Treatment: $F(1, 10) = 5.68$, $p = .038$], again in both groups (Group × Cue Identity × Cue Treatment: $F < 1$, $p = .630$). The apparent (but nonsignificant) superiority of responding to the previously reinforced cue in Group CTL versus Group BLK/OVR likely reflects the (nonsignificant) differences in responding observed at the end of discrimination training (Fig. 5).

Discussion

No evidence was apparent for blocking or overshadowing of either lever-press or food cup responding to the lever cues by either the reinforced or nonreinforced auditory cues, in either Phase 2 training or testing. It could be argued that our design worked against the observation of overshadowing: In the BLK/OVR condition, the overshadowing cue had been trained as a CS–, and hence might have encouraged "superconditioning" of the target cue (Rescorla, 1971, 2004). However, if that were the case, then this design must also be considered as providing an especially liberal assessment of blocking. Given the substantial blocking and overshadowing of auditory cue conditioning by lever cues observed in Experiments 1 and 2, the absence of evidence for these phenomena in Experiment 3 shows blocking and overshadowing between these auditory and lever cues to be decidedly asymmetrical.

One account for this asymmetry is that the content of reward learning differs depending on the choice of CS. Chang and colleagues (Chang et al., 2012a, 2012b) suggested that lever cues that support biting and other consummatory responses recruit additional neural systems beyond those engaged by diffuse auditory stimuli, or encourage learning about additional features of the food US, such as its hedonic or taste properties, which are not normally associated with diffuse cues. In those cases, during compound conditioning, such unique systems or special features would be unengaged or unpredicted by auditory cues, and hence equivalent lever-press acquisition would be predicted in all of the training conditions of Experiment 3. Experiment 4 addresses this possibility.

Experiment 4

If the asymmetries in blocking and overshadowing in Experiments 1–3 were due to engagement of unique neural systems by lever cues, or association of lever cues with unique properties of the food US, then one would expect normal blocking and overshadowing when lever cues were used as both producers and targets of blocking and overshadowing. By contrast, the failure to observe blocking or overshadowing of one lever by another might suggest that lever cues are not subject to normal stimulus selection phenomena.

Experiment 4 used a between-subjects design to evaluate blocking and overshadowing of conditioning to a lever-extension cue by another lever-extension cue. Rats first received discrimination training between lever extension and a

white noise. In this training, either extension of a lever was reinforced and a white noise was nonreinforced (L1+, N–), or lever extension was nonreinforced and the noise was reinforced (L1–, N+). Next, the rats in Groups BLK and OVR received compound lever presentations in which both the left and right levers were extended simultaneously and paired with food delivery (L1L2+). For rats in Group BLK, L1 had been previously reinforced and for rats in Group OVR, L1 had been previously nonreinforced. The remaining rats (CTL) received simple pairings of the new (L2) lever with food. Finally, responding to each of the levers was assessed separately. If prior reinforced training of L1 blocked conditioning to the added L2 lever, then one would expect less responding to L2 in Group BLK than in Group OVR. If the presence of another, previously nonreinforced lever (L1–) overshadowed conditioning to a new lever, then one would also expect less responding to L2 in Group OVR than in Group CTL.

Method

Subjects and apparatus The subjects were 26 male Long-Evans rats. The 12 naïve rats in Groups BLK and OVR were obtained and maintained as those of Experiments 1–3. The remaining 14 rats used for Groups CTL/BLK and CTL/OVR had previously been subjects in a food-rewarded T-maze experiment. These groups were trained approximately one month after Groups BLK and OVR. The apparatus was that used in Experiment 1.

Procedures Table 1 shows an outline of the procedures of Experiment 4. After a single food cup training session, in each of two 64-min sessions the rats in Groups OVR and CTL/OVR received 16 10-s presentations of the noise reinforced with the delivery of two sucrose pellets. The rats in Groups BLK and CTL/BLK received 16 10-s reinforced presentations of the right or left lever (counterbalanced) in these sessions. Next, the rats received six 64-min discrimination training sessions, each including eight 10-s reinforced presentations of the noise or lever stimulus presented in the previous sessions, interspersed randomly with eight nonreinforced 10-s presentations of the other stimulus (lever or noise). The lever used in this phase was defined as L1.

The rats in Group BLK (n = 6) and Group OVR (n = 6) then received six 64-min Phase 2 lever compound training sessions, each of which included 16 10-s reinforced presentations of both levers simultaneously. For the rats in Group BLK, one lever (L1+) had been previously reinforced, and for the rats in Group OVR, one lever (L1–) had been previously nonreinforced. The new, added lever was defined as L2. In each of these sessions, the rats in Groups CTL/BLK (n = 7) and CTL/OVR (n = 7) received 16 10-s reinforced presentations of L2, defined as whichever lever they had not received in the discrimination phase.

Test sessions that evaluated conditioning to the lever first introduced in Phase 2 (L2) were delivered after each pair of sessions in that phase. Each of these sessions included four 10-s nonreinforced presentations of L2 over 16 min. At the conclusion of the third such test, the session continued for another 16 min, in which time L1 had four nonreinforced presentations. Testing then continued to assess responding to both L1 and L2, in the absence of any reinforcers. The fourth test session was identical to the third test, except that the four L1 presentations preceded the four L2 presentations. The fifth test session also included four L1 and four L2 presentations, but they were intermixed in counterbalanced order over the 32-min test. The sixth test session included eight L1 and eight L2 trials, intermixed, in a 64-min session. The final test session was 32 min in duration and included eight L1 presentations. Thus, the entire test series (Tests 1–7) included 28 L1 and 28 L2 presentations.

Data analysis Because Groups BLK and OVR, on the one hand, and Groups CTL/BLK and CTL/OVR, on the other, were trained at different times and had different preexperimental histories, we analyzed the data from each of these two sets of groups separately. However, because their lever-press performance by the end of discrimination training did not differ, we also conducted some ANOVAs that included both sets of groups, permitting direct comparisons across conditions.

Results

One rat (in Group BLK) was identified as a goal-tracker during discrimination training and was dropped from the analyses. Figure 7 shows conditioning and discrimination phase performance, with the responding of Groups BLK and OVR in the left panels and that of Groups CTL/BLK and CTL/OVR in the right panels. During discrimination training, the rates of lever pressing (Figs. 7a and c) were higher when lever insertion was reinforced than when it was nonreinforced, in each of the two sets of rats [Fs > 10.24, ps < .008]. Considering only the final four sessions of discrimination, ANOVAs that combined the performance of both sets of rats (Groups BLK and OVR vs. Groups CTL/BLK and CTL/OVR) showed no significant effects of set [$F(1, 21) < 1$, p = .628] or interactions of set with any other variable (ps > .794), except for the Set × Session interaction [$F(3, 63) = 3.62$, p = .018]. Food cup responding (Figs. 7b and d) was acquired to high levels for the reinforced noise, but not for the reinforced levers. For each of the two sets of rats, Treatment (BLK vs. OVR) × Contingency (reinforced or nonreinforced cue) × Session ANOVAs of the food cup elevation scores showed significant effects of treatment [Fs(1, 9) > 31.83, ps < .001] and contingency [Fs(1, 9) > 28.73, ps < .001], as well as their interaction [Fs(1, 9) > 25.80, ps < .001]. An overall,

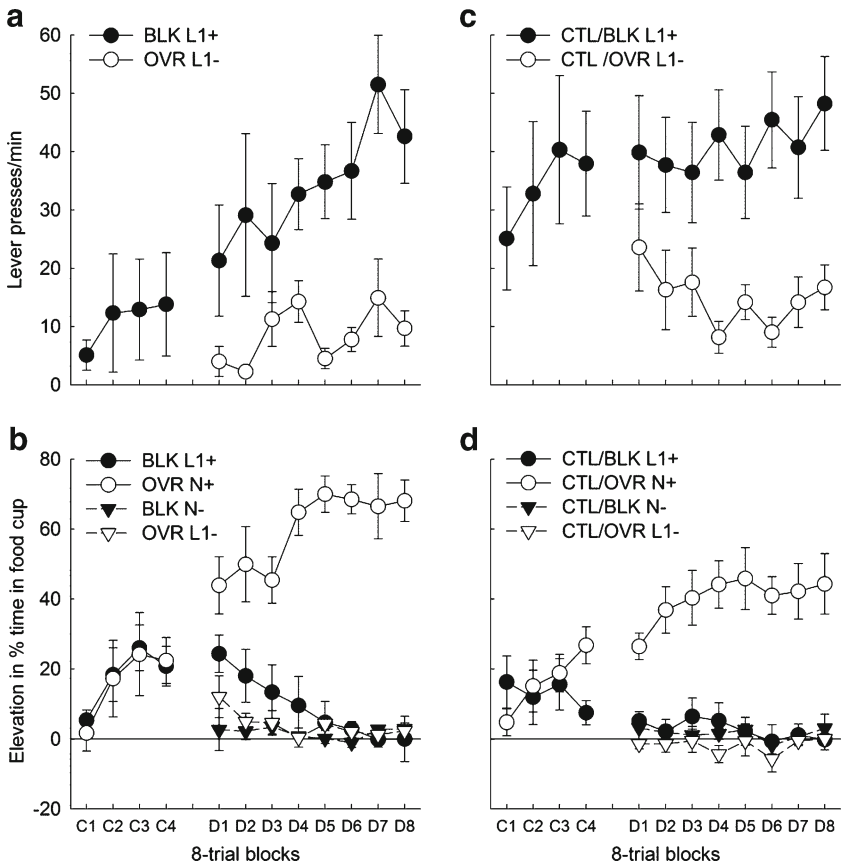

Fig. 7 Lever-press (panels **a** and **c**) and food cup (panels **b** and **d**) responding during the Phase 1 nondiscriminative (C sessions) and discrimination (D sessions) training of Experiment 4. The left panels (A and B) show responding in Groups BLK and OVR (blocking and overshadowing, respectively) and the right panels (**c** and **d**) show responding in Groups CTL/BLK and CTL/OVR (respective controls for Groups BLK and OVR). L1+ = food-reinforced lever, L1– = nonreinforced lever, N+ = reinforced white noise, N– = nonreinforced white noise. Food cup responding is expressed as the elevation of responding during cue presentations over baseline responding. All entries are means ± *SEM*s

combined ANOVA of performance over the final four sessions showed a significant effect of set [$F(1, 21) = 10.47$, $p = .004$], but no significant interactions of that variable with any other variable (ps > .071). ANOVAs of pre-CS responding, which ranged from 1.8% ± 0.9% to 4.4% ± 2.2% across groups, showed no significant effects or interactions (ps > .088).

Figure 8 shows responding during Phase 2. In this phase, rats in Groups BLK and OVR received training in which the simultaneous insertion of both levers was paired with food delivery, and the rats in Groups CTL/BLK and CTL/OVR received training in which L2 alone was paired with food. Consider first the performance of rats in Group BLK and OVR. Rats in Group BLK showed increasing responding to L2, whereas rats in Group OVR showed relatively constant levels of responding to L2 across the phase (Fig. 8a). This pattern is the opposite of what one would expect if blocking of new conditioning were occurring. By contrast, the rats in Group BLK showed decreasing responding to the previously reinforced lever (L1+), whereas those in Group OVR showed increasing responding to the originally nonreinforced lever (L1–) during this phase (Fig. 8b). ANOVAs showed that the treatment (BLK vs. OVR) × Lever × Session interaction was significant [$F(5, 45) = 3.03$, $p = .019$]. Furthermore, both the linear increase in responding to L2 and the linear decrease in responding to L1 over sessions were significant [Fs(1, 45) > 5.09, ps < .030], as was the difference between those two trends [$F(1, 9) = 8.28$, $p = .018$].

In this phase, the rats in Groups CTL/BLK and CTL/OVR received training in which L2 alone was paired with food. Responding to L2 (Fig. 8a) was acquired very rapidly during the first Phase 2 training session in both groups, but it started higher in Group CTL/BLK, which had prior reinforced training with the other lever (L1+), than in Group CTL/OVR, which had prior nonreinforced training with the other lever (L1–). Although a Treatment × Session ANOVA showed no significant effects or interactions (ps > .100), a Group × Half-Session Block ANOVA over the first session alone showed a significant Group × Block interaction [$F(1, 12) = 6.76$, $p = .023$]. Subsequent Tukey HSD tests showed lever pressing to be significantly (ps < .025) lower in Group CTL/OVR in the first half-session block (24.6 ± 6.2 responses/min) than in

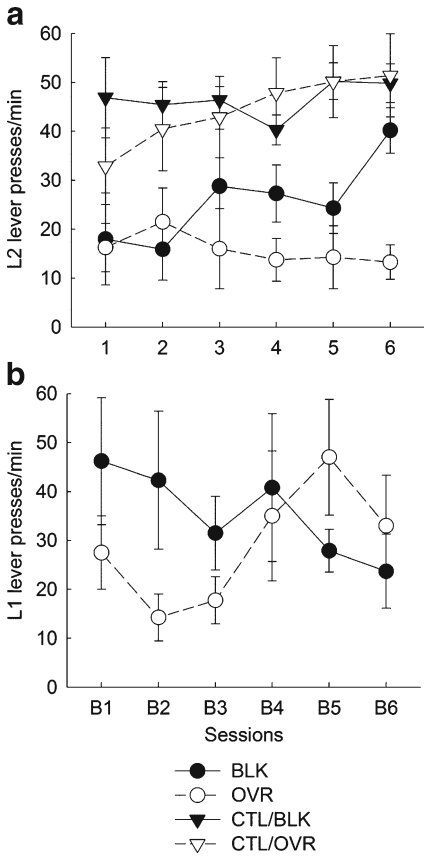

Fig. 8 Lever-press responding during Phase 2 (blocking; B sessions) training of Experiment 4. Panel **a** shows responding to L2, the lever added in that phase, and panel **b** shows responding to L1, the originally trained lever. Rats in Groups BLK and OVR received a compound of L1 and L2 in this phase, whereas rats in Groups CTL/BLK and CTL/OVR received only L2 presentations. In Groups BLK and CTL/BLK, L1 had previously been reinforced with food, whereas in Groups OVR and CTL/OVR, it had been nonreinforced. All entries are means ± *SEM*s

Group CTL/BLK (48.2 ± 8.1 responses/min) in that block, and lower than responding in either group in the second half-session block (43.5 ± 5.7 and 46.8 ± 9.1 responses/min, respectively). Finally, because the performance of the two sets of rats at the end of discrimination training was comparable, we also performed a Set × Treatment × Session ANOVA of responding to L2. That ANOVA showed a significant effect of set [$F(1, 21) = 19.29$, $p < .001$] and a three-way Set × Treatment × Session interaction [$F(5, 105) = 2.99$, $p = .015$], which reflected the overall greater pressing of L2 in the CTL groups (which had only that lever present) than in groups BLK and OVR (which had both levers present simultaneously), and the increasing superiority of responding in the BLK condition over the OVR condition versus the decreasing superiority of the CTL/BLK to the BLK/OVR condition.

There was virtually no food cup behavior prior to or during lever insertions in this phase (<6% in all conditions in any session). ANOVAs of elevation and pre-CS food cup responding, in each set of rats separately and in both together, showed no significant effects or interactions (ps > .294).

Figure 9 shows the primary data of this experiment: nonreinforced testing of responding to L2 and L1, each tested alone. We found no evidence for blocking (Fig. 9a): The rates of responding to L2 in groups BLK and OVR did not differ significantly, although a nonsignificant tendency toward greater responding in the BLK group (the opposite of blocking) did emerge. Treatment × Session ANOVAs with these two groups showed no significant effects or interaction (ps > .198). Responding to L2 also did not differ between the two CTL groups (Fig. 9a). Treatment × Session ANOVAs with these two groups showed only significant effects of session [$F(5, 60) = 2.40$, ps = .047; other ps > .143]. ANOVAs that combined the two sets of rats showed a significant effect of set [the two CTL groups showed greater responding: $F(1, 21) = 5.31$, $p = .031$] and a Set × Treatment × Session interaction [$F(5, 105) = 2.33$, $p = .047$]. Responding in Group BLK–OVR was significantly lower than responding in either of the CTL groups (ps < .034), but it did not differ from responding in Group BLK–BLK ($p = .207$).

Figure 9c shows lever-press responding to L1. Not surprisingly, responding to this lever declined over sessions in all conditions. Treatment × Session ANOVAs for each set of rats individually and for both combined all showed significant effects of session (ps < .025). Responding was greater in Group BLK, in which this lever had previously been reinforced (L1+), than in Group OVR, in which it had been nonreinforced (L1–) [$F(1, 9) = 7.39$, $p = .024$].

As in Phase 2 training, little food cup responding was evident during lever presentations in testing. However, substantial amounts of food cup behavior occurred after the levers retracted. Figure 9b shows elevation in food cup responding during the 5-s post-new-lever period, relative to the 5-s pre-CS period. Food cup responding after presentations of the added lever did not differ between the BLK and OVR treatments in either set of rats (Fs < 1, ps > .673), although an ANOVA that combined the two sets of groups showed significantly greater responding in the CTL groups [$F(1, 21) = 8.44$, $p = .009$], but no significant effects or interactions of treatment (ps > .604). Thus, as with lever pressing, we found no evidence for blocking of food cup response conditioning to the added lever in Group BLK relative to Group OVR. However, to the extent that comparisons across the two sets of rats can be trusted, there was some evidence that conditioning the added lever in the presence of another lever produced some overshadowing of food cup response learning.

Figure 9d shows food cup responding after retraction of L1 over the course of testing. Consistent with the original training of that lever, responding was greater in Group BLK (L1+) than in Group OVR (L1–) [$F(1, 9) = 8.17$, $p = .019$], and declined over sessions [$F(5, 45) = 22.58$, $p < .001$] in both of those treatment groups (Treatment × Session interaction: $F < 1$, $p = .550$). In the CTL groups, only low levels of food cup responding were ever observed after presentations of the previously nonreinforced lever (L1–) in Group CTL/OVR,

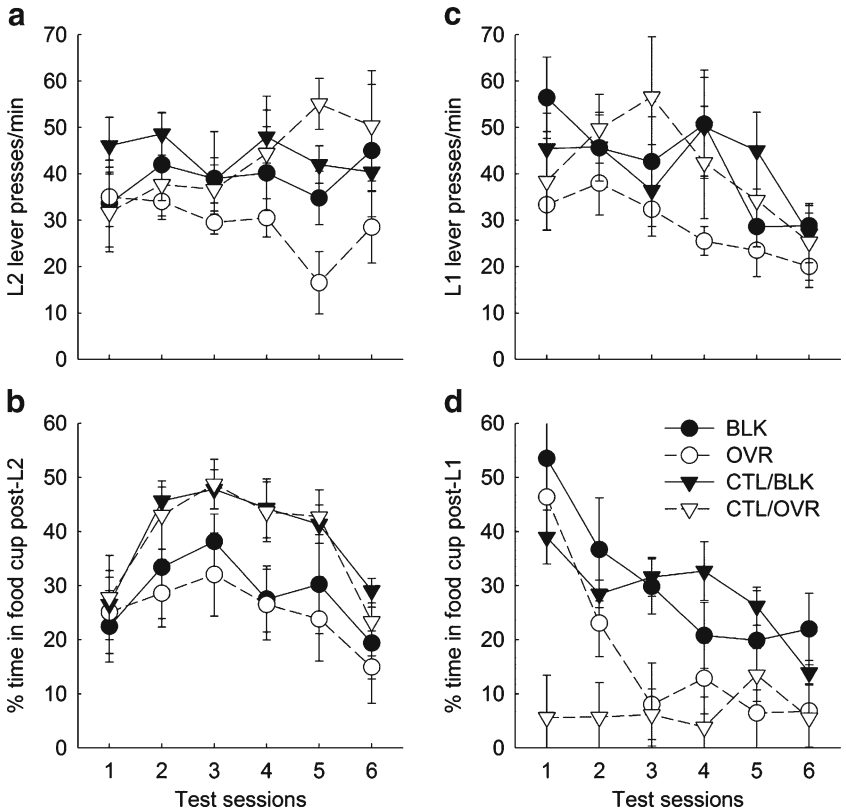

Fig. 9 Responding in the test sessions of Experiment 4. Panel **a** shows lever-press responding to L2, the lever added in Phase 2. Panel **b** shows lever-press responding to L1, the originally trained lever. Panel **c** shows food cup responding during the 5-s period after withdrawal of L2, expressed as elevation over baseline, and panel **d** shows elevation in food cup responding after withdrawal of L1. Rats in Group BLK (blocking) had previously received L1→food and L1L2→food pairings; rats in Group OVR (overshadowing) had received L1→no food and L1L2→food pairings; rats in Group CTL/BLK (control for Group BLK) had received L1→food and L2→food pairings; and rats in Group CTL/OVR (control for Group OVR) had received L1→no food and L2→food pairings. The first three tests of responding to L2 were interspersed with Phase 2 training (see the text for details). All entries are means ± *SEM*s

whereas responding to the previously reinforced lever (L1+) in Group CTL/OVR was substantial initially but declined over the course of sessions. An ANOVA showed a significant effect of treatment [$F(1, 12) = 42.59$, $p < .001$], a marginally significant effect of session [$F(5, 60) = 2.34$, $p = .053$], and a significant Treatment × Session interaction [$F(5, 60) = 2.94$, $p = .019$]. An ANOVA that combined both sets of treatment groups showed significant effects of set [more responding in Groups BLK and OVR, in which this lever had been paired with food in Phase 2, than in the CTL groups, in which this lever was not presented in that phase: $F(1, 21) = 4.92$, $p = .308$], treatment [$F(1, 21) = 39.81$, $p < .001$], and session [$F(5, 105) = 16.59$, $p < .001$], and significant Set × Session [$F(5, 105) = 9.07$, $p < .001$] and Set × Treatment × Session [$F(5, 105) = 2.39$, $p = .043$] interactions. Each group differed significantly from each other group (ps < .013), except that Groups BLK and CTL/BLK did not differ ($p = .656$).

Discussion

There was no evidence for blocking of conditioning to one lever by prior training of another lever. Indeed, in both Phase 2 training and testing, rats in Group BLK showed more responding to the added L2 lever than rats in Group OVR, the opposite of blocking. Furthermore, as responding was acquired to L2 in Group BLK, responding to the previously trained L1+ lever declined, as if the new conditioning was at the expense of the old. Because both the potential blocking and blocked stimuli were levers, it is difficult to account for the lack of blocking as the result of differences in the aspects of the food reinforcer with which they were associated or neural systems they engaged. In the General Discussion, we consider reasons why conditioning to lever-extension CSs might be peculiarly resistant to blocking.

By contrast, some evidence for overshadowing of conditioning to L2 a previously nonreinforced lever (L1–) developed over Phase 2 compound training sessions in Group OVR, relative to responding in the CTL conditions, in which rats were trained with L2 alone. However, performance of Group OVR was unusual, in that when the L2 was compounded with a previously nonreinforced L1 lever, more responding was acquired to L1 than to L2, the opposite distribution of new learning as was observed in Group BLK. We discuss some potential accounts for these observations in the General Discussion.

General discussion

Blocking, and to some extent overshadowing, were decidedly asymmetrical. Previously reinforced lever-extension CSs completely blocked conditioning to auditory cues, and previously nonreinforced lever-extension CSs overshadowed conditioning to auditory cues. By contrast, conditioning to lever-extension CSs was not blocked by either auditory or lever-insertion cues, and was not overshadowed by auditory cues. However, conditioning to a lever-insertion cue was somewhat overshadowed by the presence of another lever, especially in terms of food cup behavior displayed after lever withdrawal.

Although this asymmetry between lever and auditory cues in blocking and overshadowing is surprising, it can be viewed as consistent with prevailing accounts of blocking, provided lever cues are assumed to be dramatically more salient than the auditory cues used here. If at the end of the initial conditioning phase, the food reinforcer was completely predicted by lever cues but only partially predicted by auditory cues, then blocking of auditory cues by lever cues would be considerably greater than the blocking of lever cues by auditory cues. Unfortunately, given the substantially different forms of conditioned responding encouraged by these two classes of cues, it is difficult to evaluate that claim. However, it is notable that the rate at which asymptotic responding was established did not appear markedly different between lever and auditory cues (e,g., left and center portions of Figs. 3a and 5). Thus, we have no independent evidence for large differences in the salience of the lever and auditory cues, beyond the overshadowing and blocking data themselves. Furthermore, if the asymmetry in blocking was due solely to large differences in the saliences of lever and auditory cues, we would have expected to see blocking in Experiment 4, when both blocking and blocked stimuli were levers.

Speers, Gillan, and Rescorla (1980) noted that the occurrence of blocking may be obscured by the formation of associations between the blocked and blocking cues during the compound conditioning phase. Responding to the blocked cue might reflect its activation of a representation of the blocking cue, rather than its own associations with the reinforcer. However, our failure to observe blocking of conditioning to a lever cue by auditory cues does not seem readily attributable to such associations. In Experiment 3, activation of a representation of the auditory blocking stimulus by the added lever would be expected to elicit food cup responding, not lever pressing. Furthermore, the blocking asymmetry that we observed would require that within-compound associations are formed between a lever blocking stimulus and an added lever, and between an auditory blocking stimulus and an added lever, but not between a lever blocking stimulus and an added auditory stimulus, nor between an auditory blocking stimulus and an auditory added cue. It is hard to imagine a simple reason why that pattern of within-compound associations would be anticipated.

Costa and Boakes (2009) noted that apparent cases of blocking may sometimes reflect response competition, rather than "true" blocking based on associative interference. However, it is unlikely that the blocking observed in Experiments 1 and 2 reflected response competition, because we tested responding under conditions in which the levers were absent, and hence performance of potentially competing lever press responses was not possible. Furthermore, systematic behavioral observations in those experiments revealed little evidence for lever-site approach responses that might compete with food cup responding. Although one could posit the occurrence of some less obvious competing response, such a response should compete equally with food cup responding evoked by blocked, overshadowed or control cues, unless one also assumed that responses specific to the blocked cue were mediated by within-compound associations between the blocked stimulus and the reinforced lever (or the response to that lever), which could have been established during Phase 2. However, although such competition might have artificially inflated the amount of blocking observed when levers were used to block conditioning to auditory cues, it should also have artificially inflated the amount of blocking observed when one lever was used to block another. We observed no blocking in that case (Exp. 4). Nor would such response competition alone help explain why auditory cues failed to block conditioning to levers: Food cup responding should compete with lever press responding.

Another way of dealing with the asymmetry of blocking observed here is in terms of differences in the content of learning acquired when auditory or lever cues are paired with food. For example, Flagel and colleagues (e.g., Flagel et al., 2009; Flagel et al., 2010; Flagel et al., 2008) have emphasized substantial differences in the learning of rats that show predominantly sign tracking (i.e., lever contact) and those that show predominantly goal-tracking (i.e., food cup entry) in response to lever–food pairings. A reasonable extension of this view is that goal-tracking (food cup) and sign-tracking (lever-press) response systems involve relatively independent learning, making between-system stimulus selection effects less likely. In that case, our failure to observe blocking of autoshaped lever pressing by auditory cues in Experiment 3 is readily anticipated. However, such an account would also predict that levers would not block conditioning to auditory cues, contrary to our observations in Experiments 1 and 2, and that one lever would block conditioning to another lever, contrary to our observation in Experiment 4.

As we noted in the discussion of Experiment 3's results, Chang and colleagues (Chang et al., 2012a, 2012b) suggested more subtle differences in the content of learning when levers or auditory cues are paired with food. Whereas most stimuli become associated with general incentive properties of food reinforcers, stimuli such as levers that support biting and other consummatory responses might additionally be associated

with sensory/hedonic properties of food, which may uniquely support such lever-directed consummatory responses. In that case, levers could block conditioning to auditory cues, but because the unique aspects of food responsible for lever pressing would not be predicted by auditory cues paired with food, autoshaped lever pressing would not be blocked by prior training of auditory cues (see Rescorla, 1999a, for a related point). However, this approach would predict that one lever should block another lever, contrary to what we observed in Experiment 4.

Finally, it is possible is that lever cues are simply not subject to normal stimulus selection phenomena such as blocking or overshadowing. For example, they may engage neural circuitry in which learning is based on simple contiguity, rather than on reinforcement prediction errors, as is assumed in many modern theories of associative learning. Alternately, within comparator perspectives on blocking (Miller, Barnet, & Grahame, 1995; Miller & Schachtman, 1985), output from lever–food associations might not be modulated by other associations at the time of response performance.

Several additional aspects of our data that are difficult to integrate into most theories of blocking may be informative. In particular, results from each of the experiments suggested that not only were lever cues immune to blocking when they were reinforced in compound with previously trained cues, but also they appeared to draw previously conditioned responding away from other cues. First, in the overshadowing conditions of Experiments 1 and 2, although a novel auditory stimulus initially acquired conditioning when it was reinforced in compound with a previously nonreinforced lever cue, continued reinforcement of the lever + auditory cue compound resulted in the loss of that auditory cue conditioning. Second, in auditory cue testing of Experiment 3, food cup responding to an auditory stimulus paired with food in the first phase was lower if that cue had been reinforced in compound with a lever stimulus during the second (blocking) phase (BLK/BLK treatment) than if that stimulus had not been presented in the second phase (CTL/BLK treatment). Third, in Experiment 4, when a compound of the previously reinforced (L1+) and a novel lever (L2) was reinforced (Group BLK), responding to L1+ decreased as responding to L2 increased, even when only L1 was available.

This apparent "vampire" nature of lever cues under these circumstances is not readily accommodated within popular "US processing" accounts for blocking (e.g., Rescorla & Wagner, 1972; Sutton & Barto, 1981). Within these models, cues acquire associations only when followed by reinforcer prediction error [$\Delta V_X = \alpha_X\beta(\lambda - V_{agg})$]. In a blocking experiment, because the reinforcer is already well-predicted by the pretrained cue when the added cue is introduced, the added cue acquires little or no conditioning. However, these models provide no simple mechanism whereby conditioned responding, once established, would be reduced by additional compound training. Although losses in associative strength can occur with continued reinforcement when the reinforcer is overexpected (Rescorla, 1999b), blocking procedures do not typically provide the opportunity for overexpectation.

One potential solution to this problem is to appeal again to response competition. In Experiments 1 and 2, the additional reinforced lever presentations in Phase 2 might have resulted in an increased tendency to remain in the vicinity of the lever site, competing with food cup entry when the auditory stimuli were presented alone in the test sessions. Furthermore, increased CS-specific competition might be mediated by the formation of within-compound associations, as noted earlier in this discussion. In that case, presentation of the overshadowed auditory stimulus alone might evoke lever-site approach, and do so increasingly as the rate of pressing controlled by that lever increased over Phase 2 training. However, there was no evidence for such increased competition in the absence of the auditory CSs, and in Experiment 2, decreased responding to the overshadowing stimulus was accompanied by decreased, rather than increased, lever-site responses.

A more satisfactory account for these effects might be provided by certain "CS processing" accounts for blocking and other variations in variations in compound conditioning. For example, within the Pearce–Hall (1980) model, cue–reinforcer pairings are sufficient for conditioning, regardless of reinforcer prediction error ($\Delta V_X = \alpha_X\lambda$). In that model, blocking occurs because the associability (α) of a stimulus—its ability to participate in new learning—is a function of the reinforcer prediction error occurring on previous trials with that cue present ($\alpha_X \sim |\lambda - V_{agg}|$). In a blocking experiment, because the reinforcer is already well-predicted when the new cue is added, its associability should be rapidly driven down. However, if that cue were highly associable to begin with, or resistant to changes in its associability (Pearce, Kaye, & Hall, 1982), substantial association between the added cue and the US might be expected before its associability was driven low enough to resist further conditioning. Thus, only minimal blocking might be anticipated. Furthermore, the additional associative strength accruing to the added cue in these early stages of compound conditioning would produce an overexpectation of reinforcer value, setting the stage for reductions in responding over the course of compound training, as well as some recovery of associability of the previously trained blocking stimulus. The problem when accounting for our data is that of apportioning decreases in net associative strength to one cue while the strength of another cue is still rising.

Within the Pearce–Hall (1980) model, reinforcer overexpectation results in loss of conditioned responding to cues that accompanied that overexpectation via the establishment of associations with a no-US representation. If associations with US and no-US representations could be independently established, one might observe, paradoxically, substantial losses in previously established conditioning as the added cue acquired its own strength, depending on the relative rates

of association with US and no-US representations, and the apportionment of changes in these associations among the various cues present (e.g., Rescorla, 2000). For example, consider our observation in Experiment 4 that when a novel lever (L2) was reinforced in compound with the previously reinforced lever (L1) in Group BLK, conditioning to L1 declined as responding to L2 was acquired. Rescorla (2000) suggested that the distribution of learning among cues depends not only on an aggregate prediction error but also on an individual cue's prediction error. In particular, a cue whose strength is more distant from the value of the delivered reinforcer gains more benefit from that reinforcer than a cue whose strength is closer to that value. Thus, as a result of the presentation of the food reinforcer, the initially neutral L2 would gain proportionally more new excitatory strength than the previously trained L1.

At the same time, because the food was overexpected, associations could also be formed with the no-US representation. Because L1's net strength was greater than L2's, L1 would gain proportionally more inhibitory strength, that is, associations with the no-US representation. Similarly, in Group OVR of Experiment 4, when L2 was reinforced in compound with the previously nonreinforced L1, L1 might be expected to absorb more of the increases in conditioned responding, because, as a result of its Phase 1 discrimination training, it may have been a better predictor of no-food than L2. Of course, it might be argued that conditioning of L1 should be retarded relative to L2 because L1's inhibitory strength would have to be overcome before its excitatory strength could be expressed. However, it is notable that L1 had been trained as CS– within a discrimination involving an auditory CS+, which produced only food cup CRs. It is possible that inhibition to L1 might be expressed as inhibition of food cup CRs (Rescorla, 1997) only, and hence would not interfere with the display of lever-directed responses.

Recently, reports of substantial individual differences in the way rats respond to food-paired lever-insertion cues and the correlation of those differences to other behavioral traits (e.g., Flagel et al., 2009; Flagel et al., 2008; Robinson & Flagel, 2009) have garnered considerable attention. Thus, we should comment on our failure to observe such differences. Only three of 68 rats were classed as goal-trackers, and except in Experiment 1, the rats in our studies rarely responded to the food cup while a lever was present. Similarly, in four previously published autoshaping experiments from our lab, we found no goal-trackers among our 45 control- or sham-lesioned rats (Chang et al., 2012a, 2012b). Why did we find so few goal trackers, as compared to the findings of Flagel et al. (2009; Flagel et al., 2008) and others (e.g., Mahler & Berridge, 2009; Robinson & Flagel, 2009)? Our studies differed from theirs in at least three ways, including the strain of rats (we used Long-Evans, whereas others used Sprague–Dawley rats), the use of an explicit discriminative conditioning procedure, and the nature of the lever-insertion stimulus. We consider these last two, procedural, differences here.

First, in our studies, a nonreinforced CS− lever was inserted and withdrawn on discrete trials in the same manner as the CS+ lever, whereas in Flagel et al.'s (2009; Flagel et al., 2008) and Mahler and Berridge's (2009) studies, a control lever was either not used or was constantly present in the chamber. Notably, Boakes (1977) and Davey, Cleland, and Oakley (1982) found that introduction of a CS− lever enhanced the level of autoshaped responding beyond that observed with a CS+ lever alone. The use of a dynamic CS– lever rather than a static lever (or none at all) may force focus on the unique visual–spatial aspects of CS+. Second, it is possible that our rats' behavior was more dominated by lever contacts because lever insertion in our experiments was virtually silent, unaccompanied by the substantial auditory cues often associated with the operation of commercial electromechanical retractable levers used by others. A stimulus with predominately visual attributes is likely to capture more attention to those attributes than one with both auditory and visual attributes. Furthermore, because our CS– was the insertion of another lever, auditory or other cues produced by lever insertion in general would be a less valid predictor of food delivery than visual properties of CS+. By contrast, in studies in which all lever insertions are followed by food, as when a static control lever (or no control lever) is used, auditory and visual components of lever insertion would be equally valid. Given that the primary response to Pavlovian auditory cues for food is food cup entry (Holland, 1977), it is perhaps not surprising that other studies have shown more goal-tracking and less sign tracking than ours.

Here, we found little evidence that sign-tracking responses to lever-insertion cues were susceptible to blocking, by either auditory cues or other lever-insertion cues. We do not mean to suggest that all instances of sign tracking are immune to blocking. For example, Holland (1977) showed that conditioning of both CS-specific and goal-tracking responses in rats was blocked by conditioning of other CSs that generated very different CS-dependent CRs. Furthermore, substantial evidence has emerged that autoshaped key pecking in pigeons is subject to blocking by contextual cues (e.g., Grau & Rescorla, 1984; Khallad & Moore, 1996), auditory cues (Rescorla, 1989), and other key-based cues (Rescorla, 1981). Nevertheless, it is important to recognize that stimulus selection and other effects in associative learning may be influenced by the choice of events used. For example, Rescorla and Coldwell (1995) cautioned against using compounds of localized cues in pigeon autoshaping, because "perceptual interactions" among those cues precluded observation of summation and of other effects normally observed in associative learning experiments. Given the evidence that different brain systems are engaged when different kinds of cues are paired with food delivery, it is worth considering the possibility that interactions among them in learning and in

performance may follow different rules. In particular, it is intriguing to speculate that the roles of simple cue–reinforcer contiguity, as well as of individual and aggregate reinforcer prediction errors (e.g., Pearce & Mackintosh, 2010), may differ across stimulus classes.

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