Journal of Experimental Psychology:
Animal Behavior Processes
1988, Vol. 14, No. 3, 261-279

0097-7403/88/$00.75

Excitation and Inhibition in Unblocking

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In four experiments the nature of learning established with unblocking procedures in the appetitive conditioning of rats was examined. Measures of learning included response topography, effects of selective satiation, and summation and retardation tests of conditioned inhibition. One cue (A) was first paired with either a single unconditioned stimulus event, US1, or a sequence of two events, US1→US2. US2 was either qualitatively similar to (US2-Same) or different from (US2-Diff) US1. Then, a compound of A and a novel cue (X) was reinforced with US1 or US1→US2. Conditioning to X was blocked if either the single US1 or the US1→US2 sequence was used in both phases. If X accompanied an upshift in the reinforcer, from US1 to US1→US2, it acquired conditioned responding, especially when US2-Diff was used. Responding in the latter case was the consequence of both X-US1 and X-US2 associations. In Experiments 1-3, if X accompanied a downshift from US1→US2-Same to US1, it acquired conditioned responding that was based on X-US1 associations, but if it accompanied a downshift from US1→US2-Diff to US1, it acquired conditioned inhibition based on X-US2 associations. In Experiment 4, X acquired net inhibition at short US1-US2 intervals and net excitation at longer intervals, with downshifts from either US1→US2-Same or US1→US2-Diff to US1. However, the interval gradient was broader with downshifts from US1→US2-Diff. These data, and several other contradictory findings in the unblocking literature, are consistent with the views that (a) the surprising addition or deletion of US2 in unblocking experiments both facilitates the acquisition of excitatory X-US1 associations and establishes either excitatory or inhibitory, respectively, X-US2 associations, and (b) that the gradient of X-US1 facilitation is broader than that of X-US2 association.

Conditioning of one element of a reinforced compound stimulus is frequently blocked if another element of that compound has previously been paired with the reinforcer (e.g., Kamin, 1968). The phenomenon of blocking has generated an enormous array of experimentation and has spawned a variety of theories of stimulus selection (see Rescorla & Holland, 1982, for a review). Common to most of those theories is the notion that associations between a cue and a reinforcer are formed on a conditioning trial only if the subject is surprised on that episode. Thus, in a blocking experiment, because the reinforcer is anticipated on the basis of the prior training of one cue, little additional learning would occur during compound presentations. On the other hand, if the reinforcer is made surprising during compound presentations—for example, by omitting the prior training or delivering a different reinforcer—substantial learning is observed (e.g., Kamin, 1968).

The role of surprise has been conceptualized in various ways. Perhaps most explicit is the treatment of Rescorla and Wagner (1972). They proposed that the effective value of a reinforcer on a compound conditioning trial is a function of the discrepancy between the maximum conditioning power of that reinforcer and the current associative strength of the compound. Thus, the more the subject is surprised by the reinforcer, the greater the opportunity for learning. If that discrepancy is positive—that is, if the nominal reinforcer is poorly anticipated on the basis of the compound cues—then excitatory conditioning will occur. If that discrepancy is negative—that is, if the total strength of the compound cues is greater than that supported by the nominal reinforcer—then inhibitory conditioning will occur. Thus, within this theory, the reinforcement value of an event is derived from its surpise value, the discrepancy between anticipated and actual value of the event received.

Other theories have suggested that surprise is more loosely related to reinforcement value. Within those theories, surprise is necessary for learning to occur but does not itself determine reinforcement value. For example, Kamin (1968) proposed that posttrial surprise is necessary to engage an associative process that allows the linking of events still resident in a transient memory of the trial. Similarly, Mackintosh (1975) and Pearce and Hall (1980) suggested that posttrial surprise is necessary to maintain the associability of the conditioned stimuli (CSs) present on a conditioning trial. If the unconditioned stimulus (US) is anticipated, the associability of the added CS drops, preventing it from becoming associated with the reinforcer.

Most attempts to distinguish between these notions of surprise have used an "unblocking" procedure. First, one CS is reinforced with a particular US. Then, a compound of A and another cue (B) is reinforced with another US, typically differing from the first US in magnitude. For example, Dickinson and Mackintosh (1979) and Holland (1984b) shifted

This research was supported by grants from the National Institute of Mental Health and the National Science Foundation. I thank James Petrick, Won T. Oh, and, especially, Eydie Marmins for their considerable technical assistance with these experiments, and Mark Stanton for his helpful comments.

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the US from one food delivery to two successive food deliveries, or from two food deliveries to one, when the compound was introduced. The Rescorla-Wagner model assumes that the addition or omission of the second food delivery changes the reinforcing value of the US, either enhancing it (in the former case), permitting additional excitatory conditioning, or reducing it, generating inhibitory conditioning. Thus, it is the surprise or discrepancy provided by the changed, *second* event that is associated with the added CS. Conversely, theories like Kamin's (1968) or Mackintosh's (1975) claim that the primary role of the added or omitted event is to promote processing of the CS and the *first* event.

Dickinson and Mackintosh (1979) and Holland (1984b) observed excitatory conditioning of the added cue after both upward and downward shifts in the number of food deliveries. The conditioning of the added cue after the number of USs was shifted upward is consistent with both notions of surprise: Association of that cue with either the first or second food delivery would generate conditioning. But the observation of excitatory conditioning with downward shifts in the magnitude or quantity of the US is clearly incompatible with Rescorla and Wagner's (1972) view: The omitted second food delivery should have produced inhibitory conditioning. Instead, that omission apparently facilitated the association of the CS with the first food delivery.

However, enthusiasm for this facilitory role of surprise must be tempered by the fact that some alterations in the US do not result in excitatory conditioning of the added cue in unblocking experiments. Some changes establish inhibition to the added cue. For example, whereas Dickinson, Hall, and Mackintosh (1976) found that a reduction in the number of shocks delivered resulted in excitatory conditioning, Wagner, Mazur, Donegan, and Pfautz (1980) and Cotton, Goodall, and Mackintosh (1982) found that a reduction in the intensity of a single shock established inhibition to the added cue. Similarly, Mackintosh and Cotton (1985) found that a reduction in the concentration of a sucrose solution US produced inhibitory conditioning of the added cue. Other changes apparently produce no detectable conditioning. Bakal, Johnson, and Rescorla (1974) found that qualitative shifts in the US (from shock to loud noise or vice versa) produced no more conditioning than would be anticipated on the basis of the two USs' differences in magnitude. Similarly, Dickinson and Mackintosh (1979) found no evidence for conditioning of the added CS element if a reinforcer that comprised a sequence of two qualitatively different events (e.g., food→shock) was shifted to one that comprised only the first event (e.g., food) or if the single-event reinforcer was shifted to the two-event sequence. That outcome forced Dickinson and Mackintosh to suggest that only if the added or omitted event was "related" to the first reinforcer would it facilitate the association of that first reinforcer with the added CS.

The experiments reported here investigated the functions of the added (or omitted) event in unblocking procedures. They used procedures like those of Dickinson and Mackintosh (1979). Rat subjects received either upshifts (A→US1 and then AX→US1→US2) or downshifts (A→US1→US2 and then AX→US1) in the number of reinforcers when the compound cue was introduced. As in Dickinson and Mackintosh's (1979) experiments, US1 and US2 were either similar or dissimilar. Unlike in their experiments, however, the two reinforcers used here were both appetitive. The use of two similarly valued reinforcers reduces the complications produced by the use of reinforcers with mutually inhibitory effects (e.g., Dickinson & Dearing, 1979; Fowler, 1978).

These experiments addressed three questions. First, how US-specific are the effects of posttrial surprise? Do upward and downward shifts in the number of reinforcers produce excitatory conditioning of the added cue when the reinforcer sequence contains qualitatively dissimilar events, as well as when it contains similar ones? Second, what is the content of the associations established to X? In the case of upshifts, is the added CS associated with the first event (as suggested by Kamin, 1968; Mackintosh, 1975; and Pearce & Hall, 1980), the second event (as suggested by Rescorla & Wagner, 1972), or both? In the case of downshifts, does X form excitatory associations with the first event (e.g., Mackintosh, 1975), inhibitory associations with the omitted second event (Rescorla & Wagner, 1972), or excitatory associations with the omitted event (Ayres & Vigorito, 1984). Third, why have some downshifts in US value resulted in excitation, some in inhibition, and some in no detected change?

Experiment 1

The first goal of Experiment 1 was to determine whether shifts from a one-event to a two-event reinforcer sequence, or vice versa, generate excitatory conditioning of an added cue when the reinforcer sequence comprises two qualitatively dissimilar, but similarly valued, events. The two US events chosen (sucrose solution and solid food pellets) were known from previous, unpublished experiments in my laboratory to be of similar appetitive value, but to be readily discriminated and to generate conditioned responses with somewhat different topographies.

The second goal was to determine the nature of the learning about the added CS when dissimilar event sequences were involved. Two methods were used to determine whether X was associated with US1 or US2. First, the topography of the CR evoked by X was observed. Second, the magnitude of conditioned responding evoked by X was observed while the subjects were sated with either US1 or US2. Satiation with US1 should produce large decrements in conditioned responding if X was associated with US1 but little or no decrement if X was associated with US2 (e.g., Rescorla, 1978). Furthermore, if conditioned responding generated by X's association with one US event was masked by responding based on the other US event, the masked responding should be revealed when the masking responding is reduced by satiation (Holland, 1985a).

Method

Subjects and apparatus. The subjects were 64 male Sprague-Dawley rats obtained from the Holtzman company. They were 165 days old at the beginning of the experiment and had participated in simple operant lever-press discrimination experiments in an undergraduate laboratory class. The rats were housed in individual cages in a colony

room that was illuminated from 6:00 a.m. to 8:00 p.m. Experimental sessions were conducted between 8:00 a.m. and 4:00 p.m. Throughout most of the experiment, the rats had free access to water and were maintained at 80% of their free feeding weights by limiting their access to food. Exceptions to this schedule are noted in the description of the procedures.

Eight experimental chambers, each 22.9 × 20.3 × 20.3 cm, were used. The two end walls of each chamber were aluminum, and the side walls and top were clear acrylic. A dimly illuminated food cup was recessed behind a 5 × 5-cm opening in the center of the right end wall, 2 cm above the floor; an identical sucrose cup protruded 4 cm from the center of the left end wall, 2 cm above the floor. A 6-W, 110 VAC jeweled panel light 6 cm above the recessed food cup provided a source of background illumination. The chamber floors were made of 0.48-cm stainless steel rods spaced 1.9 cm apart. Each experimental chamber was enclosed in a sound-resistant shell. A speaker for delivering auditory stimuli and a 6-W, 110 VAC houselight (normally off), which served as one of the conditioned stimuli, were mounted on the inside wall of the shell, 10 cm above and behind the experimental chamber, even with the left end wall. An exhaust fan mounted on each shell provided air circulation and a constant masking noise (72 db SPL, measured 2 cm in front of the food magazine). The front wall of each shell contained an acrylic window to permit behavioral observations. Two low-light television cameras were mounted 2.1 m from the experimental chambers so that each could include four chambers in its field of view. Video-cassette recorders were programmed to record behaviors occurring during, and 10-s before and after, CS presentations.

Behavioral observation procedures. All observations were made from videotapes. Each rat's behavior was observed at 1.25-s intervals during the 10-s period immediately prior to CS presentations and during the CS presentations. The observations were paced by auditory signals recorded on the videotapes. On each observation one and only one behavior was recorded. Five behavioral categories were reported: *magazine*—standing motionless in front of the food magazine with head or nose within the recessed food cup; *cup*—standing motionless in front of the extending sucrose cup while contacting that cup with face or forelimbs; *head jerk*—short, rapid horizontal and/or vertical movements of the head; *rear*—standing on rear legs, with both front legs off the floor, but not grooming; and *startle*—a rapid jump or change in position (see Holland, 1977, for more complete descriptions). In addition, for rear and head jerk behaviors, I recorded the direction the rat was facing (toward the foodcup, the sucrose cup, or neither). Two observers agreed on 746 of 800 joint observations during test sessions.

The frequency of each behavior, except startle, was divided by the total number of observations made to obtain the measure *percentage total behavior.* Note that this index is an absolute measure, not a relative one, because the number of observations per stimulus is constant. The data are expressed as percentages of total observations rather than as absolute frequencies to facilitate comparisons with data of other experiments in which the total number of observations differed from that made in these experiments. Because startle responding typically occurred only once in a single trial, at CS onset, the measure of that behavior was the percentage of trials on which startle was observed.

Neither startle nor head jerk behavior was ever observed to occur during pre-CS periods. Rear and the two goal-related behaviors, cup and magazine, seldom constituted more than 6% (each) of the total pre-CS behavior in these experiments and never differed reliably between groups. Consequently, pre-CS behavior is not described.

Experimental procedure. Before the experiment, all subjects received a single, 15-min session in which four deliveries of one 45-mg food pellet (P. J. Noyes Co.) and of 0.3 ml of 0.1-M sucrose solution were intermixed randomly.

Table 1 shows an outline of the major procedures of Experiment 1. The experiment was conducted in two replications, which differed only in the nature of the reinforcers used.

Table 1
Outline of Procedures for Experiments 1–3

Group	Phase 1	Phase 2	Test 1	Test 2
		Experiment 1		
Up	A→US1	AX→US1→US2Diff	X	X (sated)
Down	A→US1→US2Diff	AX→US1	X	—
High	A→US1→US2Diff	AX→US1→US2Diff	X	—
Low	A→US1	AX→US1	X	—
		Experiment 2		
Up-Same	A→US1, B→US1→US2Same	AX→US1→US2Same, B→US1	X	X (sated)
Down-Same	A→US1, B→US1→US2Same	A→US1→US2Same, BX→US1	X	X (sated)
Up-Diff	A→US1, B→US1→US2Diff	AX→US1→US2Diff, B→US1	X	X (sated)
Down-Diff	A→US1, B→US1→US2Diff	A→US1→US2Diff, BX→US1	X	X (sated)
High-Same	A→US1, B→US1→US2Same	A→US1, BX→US1→US2Same	X	X (sated)
Low-Same	A→US1, B→US1→US2Same	AX→US1, B→US1→US2Same	X	X (sated)
High-Diff	A→US1, B→US1→US2Diff	A→US1, BX→US1→US2Diff	X	X (sated)
Low-Diff	A→US1, B→US1→US2Diff	AX→US1, B→US1→US2Diff	X	X (sated)
		Experiment 3		
Up	A→US1, B→US1	AS→US1→US2S, BD→US1→US2D	S, D	C→US1/US2, CD, CS
Down	A→US1→US2S, B→US1,US2D	AS→US1, BD→US1	S, D	C→US1/US2, CD, CS
High	A→US1→US2S, B→US1→US2D	AS→US1→US2S, BD→US1→US2D	S, D	C→US1/US2, CD, CS

Note. US1 and US2 were food pellets and sucrose, fully counterbalanced. US2Same (US2S in Experiment 3) was qualitatively similar to US1 (i.e., both food pellets or both sucrose), but US2Diff (US2D in Experiment 3) was different from US1 (i.e., one was sucrose and the other was food pellets). In Experiment 1, A was the houselight conditioned stimulus, and X was the tone. In Experiment 2, A and B were houselight and panelight, fully counterbalanced, and X was the tone. In Experiment 3, A and B were houselight and panelight, fully counterbalanced, S and D were tone and noise, fully counterbalanced; and C was the clicker. In Test 2 of Experiment 3, C was paired with US1 in half of the rats in each group and with US2 in the other half.

First, all subjects received conditioning of a 10-s flashing (3 hz) houselight. Illumination of the houselight was paired with a single US in Groups Up and Low. For half of the rats in each of those two groups (Replication 1), the US was a single 45-mg food pellet, and for the other half (Replication 2), it was the delivery of 0.1 ml of 0–2-M sucrose. In Groups Down and High, the houselight was paired with a sequence of 2 USs. For half of the rats in each of those two groups (Replication 1), the US sequence comprised one 45-mg food pellet followed 5 s later by 0.3-ml sucrose, and for the other half (Replication 2), it comprised 0.1 ml of sucrose followed 5 s later by two 45-mg food pellets. Each of the ten 80-min sessions included eight houselight–reinforcer pairings.

Next, all subjects received five 80-min sessions in which a 10-s compound of the flashing houselight and a 1500-hz, 78 db tone was paired with either a single US or a US sequence. There were eight pairings in each session. In Groups High and Low, the reinforcer was the same as that used in the houselight conditioning phase. In Group Down, the reinforcer consisted of only the first US that had been presented in the US sequence in the previous phase. In Group Up, the reinforcer was either the 1 pellet→0.3-ml sucrose (for those rats that had received the pellet-only US in the previous phase) or the 0.1-ml sucrose→2 pellets sequence (for those rats that had previously received the sucrose-only US).

Then, all subjects received a single 80-min test session in which eight nonreinforced 10-s tones were presented while the subjects were maintained at 80% of their ad lib body weights, as in training. Finally, the subjects in Group Up received two selective satiation tests, in which responding to the tone was examined while they were temporarily sated on one or the other of the USs. This phase took 3 days. On the Day 1, the rats were satiated on one food, and on Day 3 they were satiated on the other. On Day 2, the rats remained in their home cages in order to recover their 80% weights. Half of the rats received pellet satiation first, and half received sucrose solution satiation first.

Each satiation test involved seven steps. (a) Either the food magazines or the sucrose cups were filled to capacity (approximately 100 pellets or 20 ml of sucrose), and the rats were placed in their experimental chambers for 60 min while two-pellet food deliveries or 0.3-ml sucrose deliveries were given every 90 s. (b) The rats were removed from the chambers for 10 min (during this and later periods away from the experimental chambers, the rats were placed in the small holding cages that were normally used to carry the rats to and from the colony room). (c) The rats were replaced in the chambers, and deliveries of the appropriate reinforcer were given every 90 s for 15 min. (d) The rats were removed for 10 min. (e) The rats were returned to the chambers, and eight nonreinforced presentations of the tone were given over the next 80 min. (f) The rats were removed from the chambers for 10 min. (g) The rats were returned to the chambers for a 5-min consumption test. Both 15 ml of sucrose in the cup and 25 pellets in the food hopper were available simultaneously during this test.

Data analysis. The data were subjected to 2 × 4 analyses of variance (ANOVAs) with replication and group as factors. For these and all subsequent analyses, magazine and cup behaviors were combined to form the categories US1-goal behaviors and US2-goal behaviors, depending on whether US1 was food and US2 was sucrose (Replication 1) or the converse (Replication 2). Similarly, head jerk behavior was specified as oriented toward the sources of US1, US2, or neither. There were no reliable ($Fs \leq 1.29$) main effects or interactions involving the replication factor in any of the analyses. Here and subsequently, individual comparisons were made, consistent with the hypotheses of the experiments and using unpooled error terms. Distribution-free statistical methods were used when there was no variance in the scores of one or more groups. A $p < .05$ (two-tailed) level of significance was adopted.

Results

Phase 1. In Phase 1 training of the houselight, all rats acquired rear and US1-goal behaviors (either magazine, if US1 was food, or cup, if US1 was sucrose), and those that had received the US1→US2 sequence also acquired US2-goal behaviors (cup or magazine, as earlier). In the last two sessions, the rats that received only US1 (Groups Up and Low) showed 31% rear behavior, 49% US1 behavior, and 2% US2 behavior. The rats that received the US1→US2 sequence (Groups Down and High) showed 28% rear, 40% US1 behavior, and 15% US2 behavior. US2 behavior was reliably more frequent in the latter two groups combined than in the former two, $t(62) = 2.79$.

Phase 2. The left panels of Figure 1 show the behaviors that were acquired in Phase 2, when the tone was added to the houselight. Head jerk (top panel) and startle (bottom panel) behaviors, indicative of conditioning to the tone (e.g., Holland, 1977), reached substantial levels only in Group Up, in which the US was shifted from US1 alone to a US1→US2 sequence in Phase 2. Over the last two sessions, Group Up showed reliably more head jerk and startle behaviors than

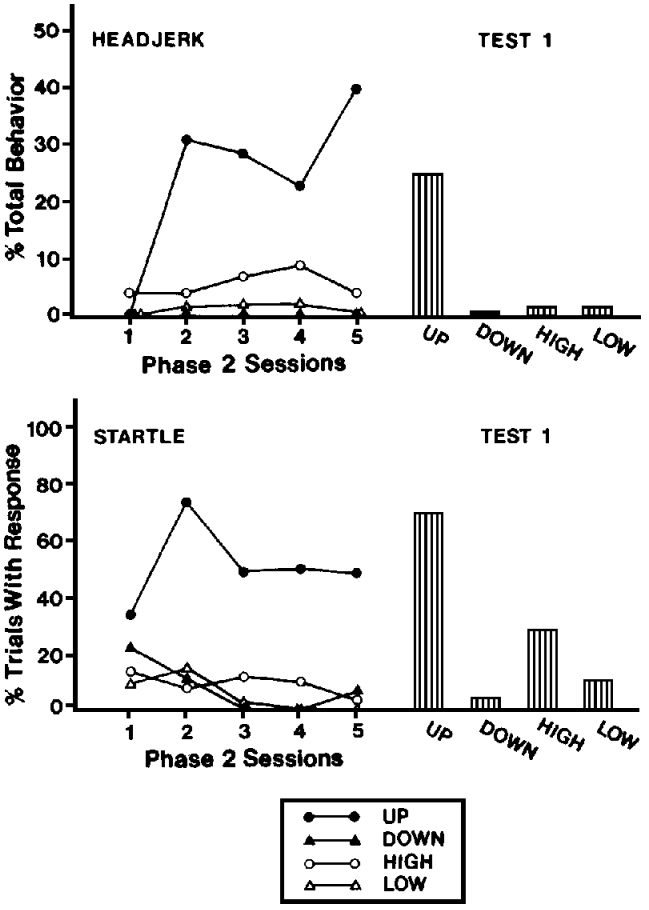

Figure 1. Mean percentages of head jerk and startle behaviors during Phase 2 and Test 1 of Experiment 1.

any of the other groups, $ts(30) \geq 5.80$, which did not differ significantly, $ts(30) \leq 1.58$.

US2 behavior presumably reflected association of either tone or houselight with US2. After an initial drop, that behavior was maintained in Group High, which received US2 in both Phases 1 and 2. Similarly, that behavior was acquired in Group Up, which received US2 for the first time in Phase 2. Conversely, US2 behavior dropped to minimal levels in Group Down, which received US2 only in Phase 1, and remained at zero in Group Low, which never received US2. Over the final two sessions of Phase 2, US2 behavior was significantly more frequent in Group Up (12%) and Group High (12%) combined than in Groups Down (2%) and Low (1%) combined, $t(62) = 2.75$.

Test 1. The right panels of Figure 1 show behavior evoked by the tone alone in Test 1. The tone evoked conditioned responding only in Group Up. Both head jerk and startle behaviors were reliably more frequent in Group Up than in any of the other three groups, $ts(30) \geq 2.73$; neither behavior differed reliably among any of the other groups, $ts(30) \leq 1.92$. Thus, relative to subjects that received either US1 alone or US1→US2 sequences in both phases, an upward shift from US1 to a US1→US2 sequence permitted conditioning of the added tone, but a downward shift from that sequence to US1 alone did not.

The test data just described do not differentiate between tone–US1 and tone–US2 conditioning, because both startle and head jerk are supported by both USs. However, further analyses of the Test 1 data suggest that both sorts of associations were formed in Group Up. Consider first the evidence that the added tone was associated with US2. First, 9 of the 16 rats in Group Up exhibited at least one instance of head jerk that was oriented toward the US2 source, but none of the rats in the other groups did (Mann Whitney $Us = 56$). Second, US2 behavior during the tone was more frequent in Group Up (5%) than in Groups Low (0%; $U = 24$) or Down (0%, $U = 31$). Although US2 behavior of Group Up did not differ reliably from that of Group High during the tone itself (4%, $U = 121$), US2 behavior during the 5-s interval after the tone was reliably greater in Group Up (13%) than in Group High (7%), $t(30) = 2.32$, as well as in Groups Low and Down (1% in both groups), $ts(30) > 5.30$. That measure of US2 behavior may be more sensitive than US2 behavior during the tone itself because in training, US2 was delivered 5 s after the end of the tone.

Test 1 also indicated that the tone was associated with US1 in Group Up. The bulk of the head jerk behavior in that group was oriented toward the source of US1; that group showed significantly more US1-oriented head jerk behavior (19%) than any of the other groups ($\leq$ 1%), $ts(30) \geq 2.61$. Similarly, US1-goal behaviors (cup or magazine) were more frequent in Group Up (30%) than in Group High (10%; $U = 9$). However, the force of the US1 behavior data is reduced by the lack of reliable, $ts(30) \leq 1.79$, superiority of Group Up to Groups Low (19%) and Down (19%).

Satiation tests. Additional evidence concerning the tone's associations in Group Up was provided in Test 2, in which responding to the tone was examined while the rats in that Group were sated on either the food pellets or the sucrose solution. The satiation procedures were very effective and very selective: While food-pellet sated, the rats consumed a median of 0 of the 25 available pellets, and 15 ml of the 15-ml sucrose available, and while sucrose-sated, consumed 25 pellets and 0-ml sucrose.

Figure 2 shows responding during Test 2, the satiation test. Both startle and US1-goal behaviors were significantly more frequent when the rats were sated on US2 than when they were sated on US1 (Wilcoxon $Ts = 0$; 5 ties), and all 7 rats that exhibited head jerk behavior in Test 2 showed it only while US2-sated. These data suggest that the tone was more associated with US1 than with US2, because US1 satiation had relatively more effect on conditioned responding than US2-satiation. Nevertheless, US2-goal behavior during the tone was reliably more frequent when the rats were US1-sated ($T = 5$; 6 ties), suggesting that the tone was also associated with US2.

Discussion

There was little evidence of conditioning to a tone when it was paired with a single US1 or a US1→US2 sequence in compound with a houselight CS that had previously been paired with that same US. Shifting the reinforcer from a single US1 to a US1→US2 sequence when the tone was compounded with the previously reinforced houselight permitted the tone to acquire conditioned responding, even though US2 and US1 each supported distinguishably different conditioned behavior. Thus, the added US need not be identical to the original US for unblocking to occur when upshifts in reinforcer number are involved.

However, downshifts from a US1→US2 sequence to US1 alone did not produce conditioning to the added tone. One possible reason may be, as Dickinson and Mackintosh (1979) suggested, that US2 must be identical to US1 in order for US2 or its omission to enhance CS–US1 associations. Thus, in Experiment 1, there was no basis for conditioning of the

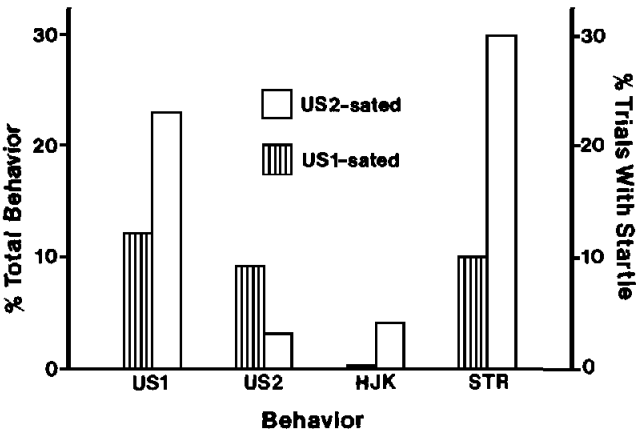

Figure 2. Behavior of Group Up during the satiation tests of Experiment 1. (US1 and US2 refer to goal behavior oriented to the source of US1 or US2, respectively, either magazine or cup behavior. HJK refers to total head jerk behavior, and STR refers to startle responding. All entries are medians.)

tone in Group Down. In Group Up, although the dissimilar US2 may not have enhanced tone–US1 association, the tone may have acquired conditioned responding by virtue of associations with US2.

Consistent with this possibility (and with the Rescorla-Wagner model's account of unblocking), upshifts from a single US1 to a US1→US2 sequence resulted in the establishment of association between the added CS and the added US2. However, two features of these data indicate that the major function served by the added US2 was to enhance associations between the tone and the original reinforcer, US1. First, most of the conditioned responding was oriented toward the source of US1. Second, conditioned responding was considerably lower after satiation on US1 than after satiation on US2. The observation that very little startle or head jerk behavior was spared by US1 satiation strengthens the claim that tone→US2 associations were relatively weak: By suppressing US1-directed behavior, US1 satiation should have revealed any US2-directed behavior that was concealed in Test 1 while the rats were deprived. Thus, the lack of acquisition in Group Down is not easily attributable to a general ineffectiveness of added or omitted dissimilar events to modulate CS–US1 associations.

A second explanation for the occurrence of unblocking with upshifts but not downshifts in Experiment 1 is simply that the use of nonidentical US1 and US2 events may reduce the amount of unblocking across the board (compared with the unblocking found when US1 and US2 are identical) and that unblocking produced by downshifts is generally weaker or more fragile than that produced by upshifts (e.g., Holland, 1985b). Experiment 2 was designed to directly compare the amounts of conditioning produced by upshifts and downshifts when the US1 and US2 events were qualitatively similar or dissimilar.

Experiment 2

The primary purpose of Experiment 2 was to compare the amounts of conditioning established to an added cue paired with upshifts or downshifts when the US1→US2 sequences involved either qualitatively similar or different events. A second purpose was to add further experimental control to the demonstration of unblocking effects. In Experiment 1, shifts in the reinforcer presented on conditioning trials were confounded with the addition or omission of those reinforcer events in the context as a whole. Those changes may have had substantial nonspecific effects, not limited to conditioning to the explicit tone CS (see Holland, 1984b; Kremer, Specht, & Allen, 1980; Neely & Wagner, 1974).

In Experiment 2, four groups of subjects received both upshifts and downshifts in reinforcement number in the compound conditioning phase. In the first phase, each rat received conditioning of two visual cues, one (A) paired with US1 alone and the other (B) paired with a US1→US2 sequence. For two groups, US1 and US2 were qualitatively different events (US1→US2-Diff), and for the other two groups, US1 and US2 were similar (US1→US2-Same). In the second phase, a tone was compounded with one of the visual cues, and the reinforcers for A and B were exchanged. Thus, in Phase 2, all subjects received an upshift after one visual cue and a downshift after the other; they differed as to which cue the novel tone was compounded with. For example, in Phase 2 in Group Up-Same, the tone was added to cue A, and the compound reinforced with US1→US2-Same, rather than US1 alone, with which A had been paired in Phase 1. Cue A + tone presentations were intermixed with presentations of B, which was now reinforced with US1 alone, rather than the US1→US2-Same sequence with which it had been paired in Phase 1.

Four additional groups of subjects also received A→US1 and B→US1→US2 presentations in Phase 1, but when the tone was added in Phase 2, the reinforcers were maintained rather than exchanged. These subjects received no upshifts or downshifts and served as blocking controls. For example, in Phase 2 in Group High-Same, the tone was added to Cue B, and the compound reinforced with US1→US2-Same, which B had been paired with in Phase 1. A→US1 pairings, also like those of Phase 1, were intermixed with the compound trials.

As in Experiment 1, responding to the tone alone was assessed both while the rats were deprived of both US1 and US2, and while they were sated on one or the other reinforcer. All eight groups of subjects received satiation tests.

Method

Subjects and apparatus. The subjects were 45 female and 19 male Sprague-Dawley rats bred from Holtzman stock in the University of Pittsburgh laboratories. All were experimentally naive, and 100–140 days old at the beginning of the experiment. They were maintained in the same way as the subjects of Experiment 1. The apparatus was the same as that used in Experiment 1.

Procedure. Initially, all subjects received two sessions designed to expose them to the pellet and sucrose deliveries. Each session was identical to the magazine training session described in Experiment 1.

Table 1 shows an outline of the major experimental procedures of Experiment 2. Experiment 2 was conducted in two replications, which differed only in the nature of the reinforcers used.

In the first phase, one visual CS, A, was paired with US1, and another, B, was paired with a US1→US2 sequence. Each of sixteen 80-min sessions contained four 10-s presentations of A and 4 of B, randomly intermixed. A and B were an intermittent (3 hz) illumination of the jeweled panelight and a continuous illumination of the houselight, completely counterbalanced across the groups. In the first replication, US1 was the delivery of 0.1 ml of 0.2-M sucrose solution. In the four groups labeled *Same,* US2 was the delivery of 0.3 ml of 0.2-M sucrose solution (US2-Same), and in the four groups labeled *Diff,* (different) US2 was the delivery of two 45-mg food pellets (US2-Diff). In the second replication, US1 was the delivery of one 45-mg food pellet; US2 was the delivery of two 45-mg food pellets in the four Same groups (US2-Same), and the delivery of 0.3 ml of 0.1-M sucrose in the four Diff groups (US2-Diff). US2 was presented 5 s after US1 in all US1→US2 sequences.

In Phase 2, all subjects received compound conditioning in which one of the pretrained visual cues was reinforced in compound with a novel 1500-hz tone, X, and the other visual cue was reinforced alone. In each of eight 80-min sessions, there were four 10-s compound presentations and four 10-s element-alone presentations, randomly intermixed. In Groups Up-Same and Up-Diff, the value of the reinforcer after the compound (AX) was shifted upward (from US1, which had been paired with A in the first phase, to the US1→US2 sequence), and the value of the reinforcer after the element alone (B)

was shifted downward (from the US1→US2 sequence, which had been paired with B in the first phase, to US1 alone). In Groups Down-Same and Down-Diff, the value of the reinforcer after the compound (BX) was shifted down, and the value of the reinforcer after the element alone (A) was shifted up. Thus all four of those groups received both upshifts and downshifts but differed as to which type of shift was paired with the novel tone (X). The remaining four groups of rats received no changes in the reinforcers paired with A and B. In Groups Low-Same and Low-Diff, X was added to A and hence was paired with the lower-valued reinforcer, and in Groups High-Same and High-Diff, X was added to B and thus was paired with the higher valued US sequence.

Next, all subjects received Test 1, a single 45-min session in which responding to four 10-s presentations of the tone alone (X) was examined. Finally, all subjects received two selective satiation tests, in which responding to the tone was examined while they were temporarily sated on one or the other of the USs. This phase took 3 days. On Day 1 the rats were satiated on one food, and on Day 3 they were satiated on the other. On Day 2 the rats remained in their home cages in order to recover their 80% weights. Half of the rats received pellet satiation first, and half received sucrose solution satiation first.

The satiation test procedure differed slightly from that used in Experiment 1: The rates of event presentations were higher, and all traces of food pellets or sucrose were removed before the test of responding to the tone. As in Experiment 1, the satiation test comprised seven steps: (a) Either the food magazines or the sucrose cups were filled to capacity (approximately 100 pellets or 20 ml of sucrose), and the rats were placed in their experimental chambers for 60 min while 2-pellet food deliveries or 0.3-ml sucrose deliveries were given every 30 s. (b) The rats were removed from the chambers for 5 min. (c) The rats were replaced in the chambers, and deliveries of the appropriate reinforcer were given every 30 s for 10 min. (d) The rats were removed for 5 min, and all traces of food pellets or sucrose solution were removed. (e) The rats were returned to the chambers, and four nonreinforced presentations of the tone were given over the next 45 min. (f) The rats were removed from the chambers for 5 min. (g) The rats were returned to the chambers for a 5-min consumption test. Both 15 ml of sucrose in the cup and 50 (rather than 25, as in Experiment 1) pellets in the food hopper were available simultaneously during this test.

Results

In Phase 1, rear and US-related behaviors were acquired to both visual cues. Unlike in Experiment 1, however, there were no reliable differences in the frequencies of those behaviors between the cues that were paired with two-US sequences and those paired with a single US (25% vs. 28% for rear, and 41% vs. 42% for US1-goal behavior; *ts* [63] < 0.37). Also unlike in Experiment 1, behavior appropriate to the US2-Diff event comprised less than 5% of the rats' total behavior and did not differ among the CSs or groups. The results of subsequent phases showed, however, that the subjects discriminated between the visual cues and between the US events.

Compound conditioning. Figure 3 shows head jerk and startle behaviors evoked by the compound CSs in Phase 2. Those two behaviors, which presumably reflect conditioning of the added auditory cue, were acquired only in the groups that received shifts in reinforcer value after the compound trials. Furthermore, upward shifts in the reinforcer enhanced conditioning of the added tone more if US2 *differed* from

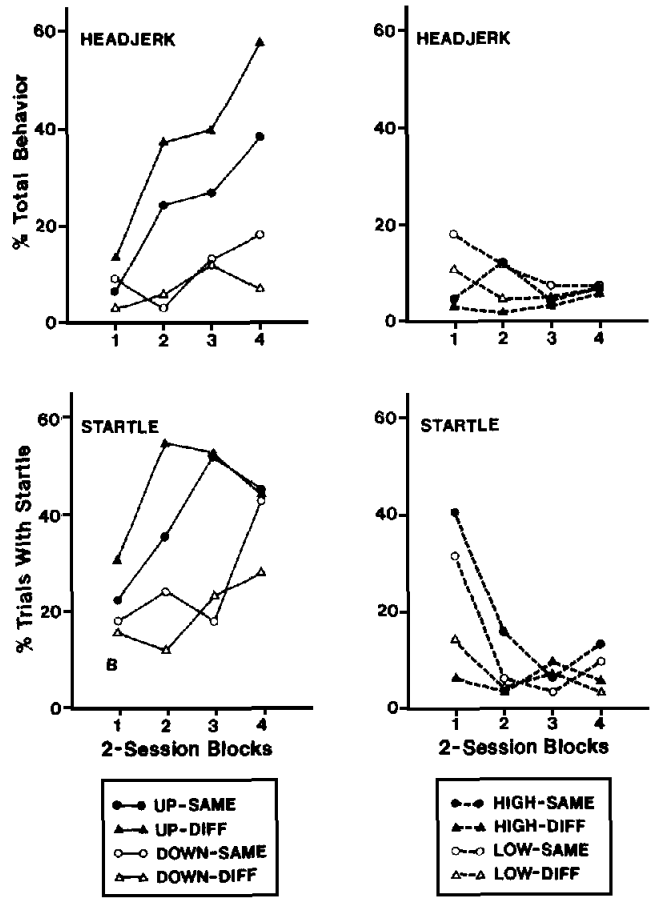

Figure 3. Mean percentages of head-jerk and startle behaviors evoked by the compound conditioned stimulus during Phase 2 of Experiment 2.

US1, but downward shifts enhanced conditioning more if US2 was qualitatively *similar* to US1.

The abrupt decline in startle responding in the unshifted groups probably reflects the habituation of unconditioned orienting behavior to the auditory cue (see Holland, 1977). In Phase 2, those subjects maintained the US1-goal and rear behaviors that were conditioned to the visual cues in Phase 1.

The data from the final two sessions of Phase 2 were first analyzed with a 2 × 2 × 2 × 2 ANOVA. The factors were (a) whether the reinforcer following the compound cue in Phase 2 was shifted or unshifted from the Phase 1 reinforcer, (b) whether the reinforcer following the compound in Phase 2 was the single US1 or the US1→US2 sequence, (c) whether the US1→US2 sequence was homogeneous (same) or heterogeneous (different), and (d) whether US1 was sucrose and US2 food (Replication 1), or vice versa (Replication 2). There were no reliable main effects of the replication factor, nor did that factor interact significantly with any other (*Fs* < 2.0). That factor was ignored in the analyses to follow.

Analyses of both head jerk and startle data showed reliable effects of the shifted/unshifted (experimental/control) factor and its interactions with the other two factors, *Fs*(1, 56) ≥ 5.71. Each of the shifted groups showed more startle behavior

than each of the unshifted groups, $ts(14) > 2.78$, and all but Group Down-Diff showed more head jerk behavior, $ts(14) > 2.22$.

Separate two-way, Single/Sequential US × Same/Different US analyses were then conducted for the shifted groups (Up-Same, Up-Diff, Down-Same, and Down-Diff) and for the unshifted groups (High-Same, High-Diff, Low-Same, and Low-Diff). There were no differences in either behavior among the unshifted groups, $Fs(1, 28) < 2.5$, but those two factors interacted among the shifted groups for both behaviors, $Fs(1, 28) > 5.19$. Head jerk behavior was more frequent in Group Up-Diff than in Group Up-Same, $t(14) = 3.01$, but more frequent in Group Down-Same than in Group Down-Diff, $t(14) = 2.16$. Startle behavior was less frequent in Group Down-Diff than in any of the other three groups, $ts(14) > 2.71$), which did not differ, $t(14) < 0.4$.

US1-goal behavior on the visual element-alone trials during Phase 2 was subjected to a similar 2 × 2 × 2 × 2 analysis. No interactions were significant ($Fs < 1.45$). The only reliable main effect was of sequential/single US, $F(1, 56) = 8.88$; the groups that received US1→US2 sequences on element-alone trials in Phase 2 (Down groups, $M = 74\%$ of total behavior; Low groups, $M = 74\%$) showed more US1-goal responding than the groups that received the single US1 on element-alone trials (Up groups, $M = 50\%$; High groups, $M = 62\%$). In addition, the Up groups, which received element-sequence US pairings in Phase 1 but element-single US pairings in Phase 2, showed reliably less US1-total behavior during the element-alone in Phase 2 than the High groups, which received the single US in both phases, $t(30) = 2.06$. This result will be considered further in the General Discussion.

Test 1. The top portions of Figure 4 show total head jerk and startle behaviors during the tone in Test 1. The tone evoked substantial head jerk and startle behavior, relative to unshifted controls, in Groups Up-Diff, Up-Same, and Down-Same, but not in Group Down-Diff. As was suggested by the Phase 2 data, upshifts that involved qualitatively *different* USs (Group Up-Diff) produced more acquisition of head jerk behavior (but not startle) than upshifts that involved similar USs (Group Up-Same). For both behaviors, downshifts that involved two qualitatively *similar* USs generated more conditioning to the tone than downshifts that involved two dissimilar USs.

The lower portions of Figure 4 show Test 1 head-jerk behavior, partitioned by its orientation—that is, whether it was directed toward the delivery site of the event used as US2-Same or that used as US2-Diff. US2-Same directed head jerk behavior, presumably indicating tone-US1 or tone-US2-Same associations, was enhanced (relative to controls) in both upshift groups and in Group Down-Same. Head jerk behavior directed toward the site of US2-Diff was enhanced only in Group Up-Diff.

The test data were subjected to statistical analyses like those described for the Phase 2 data. For all behaviors described, there were no effects of replication, nor did that factor interact reliably with any other factor.

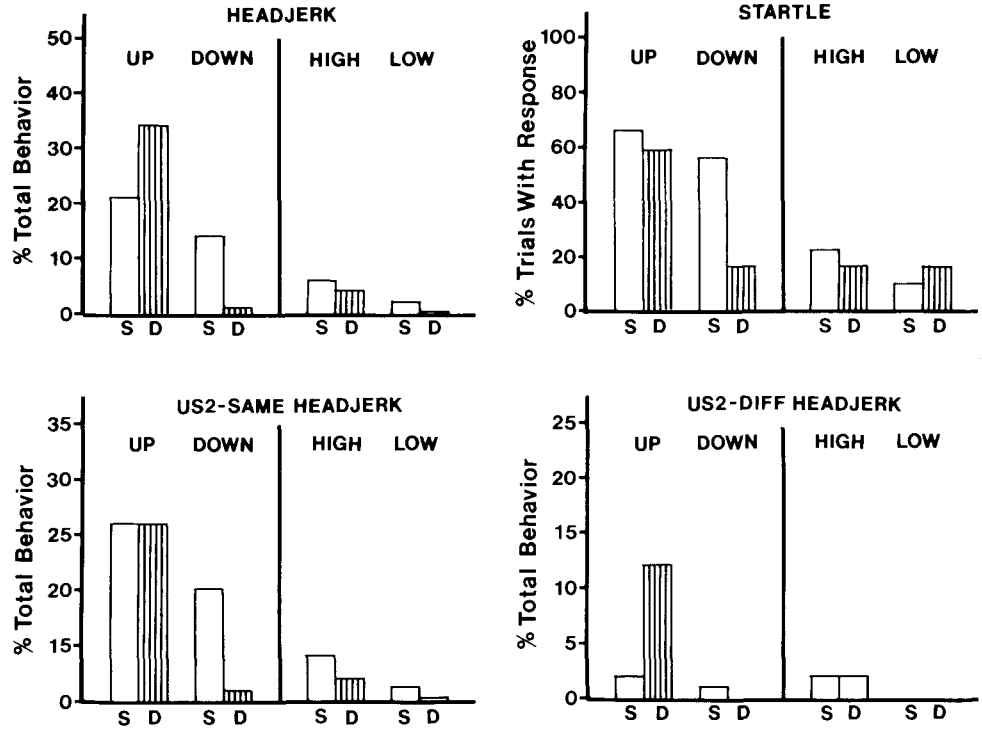

Figure 4. Head-jerk and startle behaviors evoked by the tone during the Test phase of Experiment 2. (In each panel, each bar refers to the mean performance of a single group. The groups are defined by the labels near the top of each panel and the labels on the abscissas: S = Same and D = Diff. For example, the leftmost bar in each panel reflects the performance of Group Up-Same.)

The effect of the shifted/unshifted factor, and its interactions with the other two factors, were reliable for all of the behaviors just described, $Fs(1, 56) > 4.53$. Startle, total head jerk, and US2-Same oriented head-jerk behaviors were each more frequent in Groups Up-Same and Up-Diff than in any of the unshifted groups, $ts(14) > 2.50$. Group Down-Same showed reliably more startle behavior than any of the controls, $t(14) = 2.98$, but that group's total and US2-Same-oriented head-jerk behaviors were reliably greater only than those of Groups Low-Same and Low-Diff, $ts(14) > 2.26$. None of those three behaviors was more frequent in Group Down-Diff than in any of the controls, $ts(14) < 0.34$. US2-Diff oriented head-jerk behavior was more frequent in Group Up-Diff than in any of the unshifted groups, $ts(14) > 2.90$, but none of the other shifted groups showed more of that behavior than any of the unshifted groups, $ts(14) < 1.39$.

Two-way analyses of all four behaviors showed no reliable effects or interactions among the unshifted control groups, $Fs(1, 28) < 2.51$, but showed reliable interactions of upshift/downshift and same/different US2 factors, $Fs(1, 28) > 4.69$, among the shifted groups. Total head-jerk behavior was reliably more frequent in Group Up-Diff than in Group Up-Same, $t(14) = 2.30$, but more frequent in Group Down-Same than in Group Down-Diff, $t(14) = 2.66$. Startle and US2-Same oriented head-jerk behaviors were more frequent in Group Down-Same than in Group Down-Diff, $t(14) > 2.19$, but the two upshift groups did not differ from each other. US2-Diff oriented head-jerk behavior was more frequent in Group Up-Diff than in any of the other groups, $ts(14) > 2.72$.

Neither magazine nor cup behaviors (combined as described in Experiment 1) showed reliable effects of the shifted/unshifted factor or interactions of that factor with the other two factors, $Fs(1, 56) < 1.61$, so no further analyses of those behaviors are reported.

Satiation tests. After Test 1, all subjects received test presentations of the tone CS while they were sated with US2-Same (US1) and while they were sated with US2-Diff. None of the behaviors observed here accounted for more than 5% of the total behavior of the rats in the unshifted control groups (Groups Low-Same, Low-Diff, High-Same, and Low-Diff), so I will discuss only the data from the shifted groups.

US2-Same satiation would be anticipated to reduce conditioned responding that was based on associations with US1 (or US2-Same) but to leave behavior based on associations with US2-Diff relatively unaffected. Only Group Up-Diff, which received upshifts to a US1→US2-Diff sequence, exhibited more than 2% of any conditioned behavior while sated with US2-Same. In that group, startle responding occurred on 18% of the trials, and US2-Diff directed head-jerk behavior constituted 10% of their total behavior, as would be anticipated if those behaviors were at least partially due to tone–US2-Diff associations. Both of those behaviors were significantly more frequent in Group Up-Diff than in any of the other groups ($Us \leq 6$).

Conversely, US2-Diff satiation would be expected to reduce conditioned responding that was based on associations with US2-Diff but to leave intact behavior based on associations with US2-Same (or US1). Indeed, US2-Diff satiation eliminated US2-Diff oriented head-jerk behavior in Group Up-Diff (0%) but had much less effect on the other conditioned behaviors than did US2-Same satiation. Indeed, the pattern of responding while subjects were sated on US2-Diff was similar to that in Test 1: Startle behavior occurred on 38%, 36%, 20%, and 0% of the trials in Groups Up-Same, Up-Diff, Down-Same, and Down-Diff, respectively, and total head-jerk behavior composed 20%, 16%, 12%, and 0% of the total behavior of the subjects in those groups. The absence of greater startle and/or total head-jerk behavior in Group Up-Diff than in Group Up-Same (as was found in Test 1) would be anticipated if that Test 1 superiority was due to the additional effect of tone→US2-Diff associations, because the influence of those associations should be attenuated by US2-Diff satiation.

Discussion

The results of Experiment 2 confirmed and extended the major data patterns of Experiment 1. The concomitant addition of a novel CS and a qualitatively different US2 when compound conditioning was begun enhanced association between that CS and the original US1. That enhancement was at least as great as that produced by the addition of a qualitatively similar US2. Furthermore, the presentation of US2-Diff permitted the acquisition of CS–US2-Diff associations as well. Thus, US2-Diff generated *more* conditioning (unblocking) of the added CS than US-Same.

Conversely, the *omission* of a qualitatively different US2-Diff generated *less* conditioning of the added CS than the omission of US2-Same: Only the omission of US2-Same generated reliable conditioning to the added CS. Because unblocking was more substantial with the *addition* of US2-Diff than the addition of US2-Same, the lack of conditioning with downshifts from US2-Diff can not be attributed to a general less effective influence of dissimilar events on unblocking. Nor can the differential effects of US2 similarity with upshifts and downshifts be attributed to nonspecific effects of the upshift or downshift procedures, because all experimental subjects received both upshifts and downshifts in the reinforcers in the second, compound conditioning phase, and identical experience with single US1 and US1→US2 sequence reinforcers throughout the experiment.

Experiment 3

Why was *addition* of US2-Diff a *more* effective agent of unblocking than addition of US2-Same, but the *omission* of US2-Diff *less* effective than omission of US2-Same? A variety of evidence (e.g., Terry, 1976; Whitlow, 1975) suggests that US2-Diff would be more effectively processed than US1-Same. For example, Terry (1976) found that US2 was a more effective reinforcer if it was preceded by a dissimilar US1 than by a similar US1. Wagner (e.g., 1978, 1981) suggested that a US2 is less likely to enter into associations if a representation of US2 is already activated in memory, for example, as a result of US1 presentation. Thus, it is not surprising that upshifts to sequences that included US2-Diff produced more conditioning than those that contained US2-Same. But presumably, the omission of a more potent event would be a more salient "event" than the omission of a less salient one.

Why, then, were downshifts from heterogeneous sequences *less* effective in establishing excitatory conditioning to the added cue than were downshifts from homogeneous sequences?

It seems reasonable to suppose that US2 plays both roles discussed earlier. First, it modulates conditioning based on US1. Surprising US2 presentation or omission should enhance associations between CSs and US1, either by influencing attention to the CSs (e.g., Mackintosh, 1975; Pearce & Hall, 1980) or by encouraging more effective processing of US1 (e.g., Kamin, 1968). Second, it establishes associations in its own right. Presentation of US2 should establish CS–US2 associations, and omission of US2 should establish inhibitory CS–US2 associations. Thus, with upshifts, both functions of US2 combine to generate conditioning of the added CS, but with downshifts those two functions are competitive.

Enhancement of US2's effectiveness by making it different from US1 would then unambiguously enhance conditioning to the added CS in the case of upshifts in reinforcer value when that CS is introduced, both because US2-Diff would be more effective a reinforcer for CS–US2 associations and because US2-Diff would more effectively enhance processing of the CS–US1 episode. However, in the case of downshifts, the effect of omitting more potent US2 events would depend on whether that omission more encouraged the facilitation of excitatory CS–US1 association or the formation of inhibitory CS–US2 association.

If variations in the potency of US2 more affected its ability to participate in associations with the added CS, then the omission of the more salient US2-Diff would especially enhance CS–US2 inhibitory associations without dramatically enhancing excitatory CS–US1 associations. If that inhibition transferred somewhat, so that responding due to CS–US1 associations was suppressed, then downshifts from heterogeneous US sequences would appear to generate less conditioning relative to downshifts from homogeneous sequences, because any greater facilitation of CS–US1 association would be overpowered by the much larger inhibitory conditioning.

In Experiment 3 this notion was tested by examining inhibitory, as well as excitatory, learning about the added CS in unblocking procedures. Presumably, inhibitory learning should be greater when the reinforcer is shifted down from a US1→US2-Diff sequence than when shifted down from a US1→US2-Same sequence.

Like Experiment 2, Experiment 3 compared responding after upshifts and downshifts in the reinforcer, when the sequences involved either similar or different US1 and US2 events. However, in Experiment 3, each rat received both shifts that involved heterogeneous sequences and those that involved homogeneous ones, although each rat received only upshifts or only downshifts. (In contrast, in Experiment 2, each rat received both upshifts and downshifts, but only heterogeneous shifts or only homogeneous shifts.)

Method

Subjects and apparatus. The subjects were 26 male and 22 female Sprague-Dawley rats, 120–150 days old at the beginning of the experiment. They were experimentally naive and were bred and maintained as described in Experiment 2. The apparatus was that used in Experiments 1 and 2.

Procedure. Magazine training was identical to that of Experiment 2. Table 1 gives an outline of the experimental procedures of Experiment 3, which was conducted in two replications, as were Experiments 1 and 2.

In the first phase, two visual cues, A and B, were conditioned. Cues A and B were a 10-s intermittent (3 hz) illumination of the houselight, and a 10-s continuous presentation of the panelight, completely counterbalanced. In each of fifteen 80-min sessions, four A and four B presentations were randomly intermixed. Group Up received pairings of both A and B with US1; Groups Down and High received pairings of A with a homogeneous sequence of US1→US2-Same, and B with a heterogeneous US1→US2-Diff sequence. In the first replication, US1 was 0.1 ml of 0.1-M sucrose solution, US2-Same was 0.3 ml of that solution, and US2-Diff was two 45-mg food pellets. In the second replication, US1 was one 45-mg food pellet, US2-Same was two 45-mg pellets, and US2-Diff was 0.3 ml of 0.1-M sucrose solution. In all sequences, US2 was delivered 5 s after US1.

In the second phase, an auditory cue (S or D) was added to each visual cue, and the compounds were reinforced. Cues S and D were an intermittent (3 hz) white noise or a continuous 1500-hz tone (both 78 db), completely counterbalanced. Four 10-s presentations of the AS compound and four 10-s presentations of the BD compound were given in each of ten 80-min sessions. In Group Down, both the AS and BD compounds were reinforced with US1 only. Thus, the A*S* compound was followed by a downshift from a homogeneous, "*S*ame", US1→US2-Same sequence, and the B*D* compound was paired with a downshift from a heterogeneous, "*D*ifferent", US1→US2-Diff sequence. In Groups Up and High, the AS compound was followed by the US1→US2-Same sequence, and the BD compound was followed by the US1→US2-Diff sequence. Thus, in Group Up, AS was followed by an upshift to a homogeneous sequence, and BD was followed by an upshift to a heterogeneous sequence, whereas in Group High, the US sequences used in the first phase were maintained, so no upshifts occurred.

Next, the performance to the two auditory cues alone, S and D, was assessed in all subjects. In each of three 80-min sessions, four 10-s S and four 10-s D presentations were randomly intermixed. No USs were presented in these test sessions. In addition, a single session to evaluate responding to the two visual cues alone (A and B) was administered between the second and third auditory cue test. That 80-min session comprised four 10-s presentations each of A and B, randomly intermixed and all nonreinforced.

Finally, inhibition to S and D was assessed. The measure of inhibition used was the rate of acquisition of a discrimination between a new, reinforced excitor and a nonreinforced compound of that excitor and the test cue. First, the rats received eight pairings of a 10-s clicker (7 Hz, 73 db) with a reinforcer in each of two sessions. For half of the rats in each group, that reinforcer was US1, and for half it was US2-Diff. Then, the rats received 12 sessions which comprised two reinforced presentations of the clicker alone, three nonreinforced presentations of a 10-s compound of the clicker and S, and three nonreinforced clicker + D compound presentations, randomly intermixed.

Results

Phase 1 acquisition proceeded as in the previous experiments. Figure 5 shows the Phase 2 acquisition of total head-jerk and startle behaviors, presumed to index conditioning to the added auditory cues. As in the previous experiments, those behaviors were acquired to compounds that were paired with upshifts to either same or different US1→US2 sequences

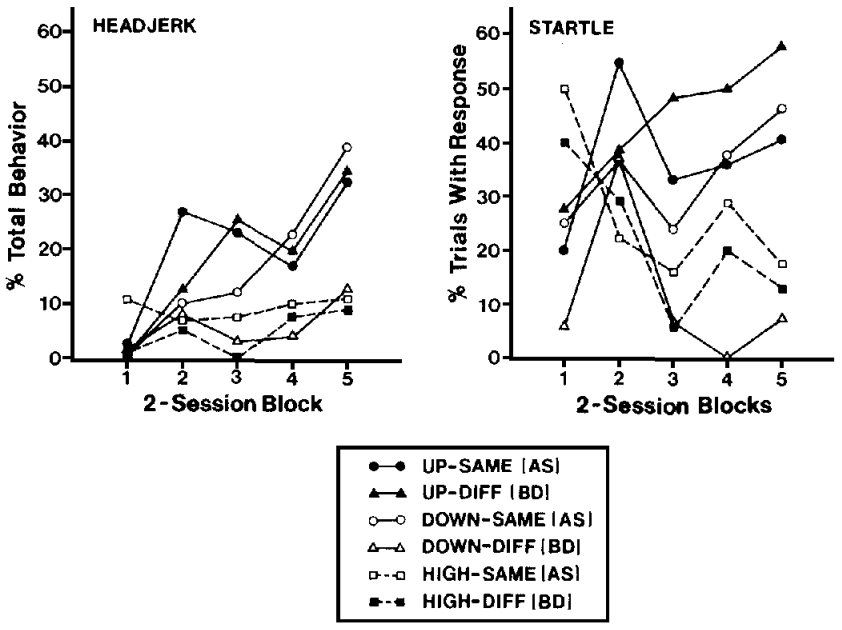

Figure 5. Mean percentages of head-jerk and startle behaviors evoked by the compound conditioned stimuli in Phase 2 of Experiment 3. (The curves are labeled by group—UP, DOWN, or HIGH—and stimulus—SAME [cue AS] or DIFF [different; cue BD].)

and to compounds that were paired with downshifts from homogeneous US1→US2 sequences, but not from heterogeneous US1→US2 sequences.

The data from the last two-session block of Phase 2 were subjected to 2 × 3 × 2 ANOVAS, with factors of replication, group, and sequence type (heterogeneous [different] vs. homogeneous [same] US1→US2 sequence). Only the effects of Group and the Group X Sequence Type interactions were reliable, $Fs(1, 42) > 25.08$. Group Up's and Group Down's performances were then compared with those of the unshifted Group High. Both compounds in Group Up evoked more of both head-jerk and startle behaviors than the corresponding compounds in Group High, $ts(30) > 4.89$, but in Group Down, only the compound that was paired with a downshift from a homogeneous sequence (AS) evoked more of either behavior than that compound in Group High, $ts(30) > 5.0$. Finally, within each group, performances to the two compounds were compared. More of both behaviors was evoked by the same compound (AS) in Group Down, $ts(15) > 7.0$, but in Group Up, more startle behavior was evoked by BD, the "different" compound, $t(15) = 2.35$. Neither behavior in Group High nor head jerk behavior in Group Up differed between the same and different compounds, $ts(15) < 1.21$.

Figure 6 shows the results of the first session of Test 1. (Little conditioned behavior was observed in the other sessions; in fact, those sessions were included in order to ensure that responding to S and D was at minimal levels at the beginning of inhibition testing). Startle behavior (top right panel) exhibited the general pattern of behavior observed in Experiment 2: Upshifts to US1→US2 sequences produced substantial responding to the added auditory cue, especially D (which had been paired with an upshift in which US2 was qualitatively different from US1). Conversely, downshifts to US1 alone produced responding only if US2 in the original US1→US2 sequence was qualitatively *similar* to US1 (Cue S). Because initial analyses showed replication differences in head-jerk behavior (described later), the graphs for that behavior are split to distinguish behavior in the first replication, in which US1 was food and US2 was sucrose (wide bars in Figure 6) from that in the second replication, in which US1 was sucrose and US2 was food (narrow bars). In the first replication, total head-jerk behavior showed a pattern identical to that just described for startle behavior: Upshifts to the US1→US2-Diff sequence produced more responding than did upshifts to the US1→US2-Same sequence, but only downshifts from the US1→US2-Same sequence produced conditioning. However, in the second replication, equivalent conditioning was found with both types of upshifts, and downshifts did not generate reliable conditioning.

The lower left panel of Figure 6 shows head-jerk behavior that was oriented toward the source of US2-Same, which presumably reflects associations between the auditory cues and the US2-Same (or US1) event. In both replications, upshifts to both same and different US1→US2 sequences produced comparable acquisition of that behavior. In the first replication, the cue in Group Down that was paired with a downshift from the US1→US2-Same sequence also acquired that behavior, but in the second replication, same-oriented head jerk was not reliably acquired to that cue.

The lower right panel of Figure 6 shows head-jerk behavior that was oriented toward the source of US2-Diff, which presumably reflects associations between the auditory cues and US2. In Replication 1, that behavior was acquired only to the cue that had been paired with an upshift to the US1→US2

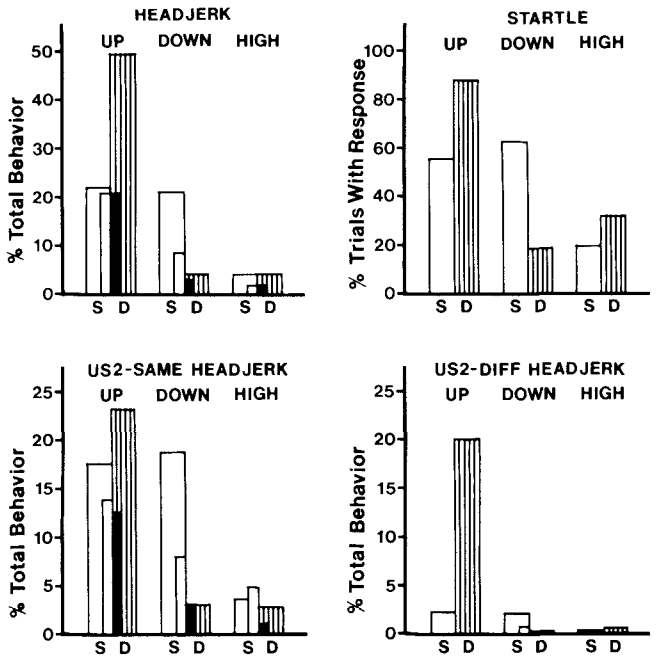

Figure 6. Mean percentages of head-jerk and startle behaviors evoked by the auditory target cues in Test 1 of Experiment 3. (The groups are labeled near the top of each panel. S and D on the abscissas refer to performance to the *S*ame and *D*iff[erent] cues. In the top right panel [startle behavior], the bars show performance summed over both replications. In the other three panels, the wider bars show performance of the rats in the first replication, and the narrower bars show performance of the rats in the second replication.)

sequence. Only minimal amounts of that behavior occurred to any cue in the second replication.

The data of Test 1 were first analyzed with 2 × 3 × 2 ANOVAs with factors of replication, group, and sequence type (same/different). For startle behavior, the only reliable effects were those of group, $F(2, 42) = 24.49$, and the Group × Sequence Type interaction, $F(2, 42) = 24.08$. The performance to each auditory cue in Groups Up and Down was then compared with that during the comparable cues in Group High. Both cues in Group Up, $ts(30) > 2.12$, and the same cue in Group Down, $t(30) = 2.96$, evoked more startle than did the cues in Group High. Startle behavior to the different cue in Group Down did not differ reliably from that to the different cue in Group High, $t(30) = -1.26$. In Group Up, startle behavior was more frequent to the different cue than to the same cue, $t(15) = 3.63$, but in Group Down, it was more frequent to the same cue than to the different cue, $t(30) = 6.21$.

For head jerk behaviors, comparable analyses revealed reliable effects of the replication factor, $Fs(1, 42) > 8.33$, and its three-way interaction with group and sequence type, $Fs(1, 42) > 10.60$. Consequently, separate analyses were performed on the data of each replication. First, behavior in the shifted groups was compared with behavior in the unshifted control, Group High. In both replications, both cues in Group Up evoked more total head-jerk behavior and more US2-Same oriented head-jerk behavior than the corresponding cues in Group High, $ts(14) > 2.40$, but the different cue in Group Down did not, $ts(14) < 0.67$. In Replication 1, the same cue in Group Down evoked more total- and US2-Same-oriented head jerk than the same cue in Group High, $t(14)s > 3.20$, but in Replication 2, it did not, $ts(14) < 0.86$. In Replication 1, only the different cue in Group Up evoked more US2-Diff-oriented head-jerk behavior than the corresponding cue in Group High, $t(14) = 5.87$; in Replication 2, even that cue failed to evoke significantly more of that behavior than found in Group High, $t(14) = 1.67$.

Next, behavior to the same and different cues was compared within each group. In Replication 1, total head-jerk behavior was more frequent during the different cue than the same cue in Group Up, $t(7) = 5.21$, but more frequent during the same cue in Group Down, $t(7) = 3.00$. US2-Same-oriented head jerk did not differ between the two cues in Group Up, $t(7) = 1.17$, but was more frequent during the same cue in Group Down, $t(7) = 2.62$. US2-Diff-oriented head-jerk was more frequent during the different cue than the same cue in Group Up, $t(7) = 7.37$. In Replication 2, there were no reliable within-group differences, although there was marginally greater US2-Same-oriented head-jerk behavior to the same cue than to the different cue in Group Down, $t(7) = 1.88$, $p < .10$.

There were no reliable effects of any factor for magazine or cup behaviors ($Fs < 2$).

Inhibition test. All subjects rapidly acquired head-jerk behavior to the clicker in Test 2, reaching asymptotes of about 50% total behavior by the fourth block of sessions. There were no differences among the groups in clicker responding.

Figure 7 shows the Test 2 acquisition of the discrimination between the clicker, and the clicker + S and clicker + D compounds. Perhaps surprisingly, there were no effects of replication in this test ($Fs < 1$). The right side shows the discrimination difference scores (clicker alone − compounds) for the rats in which the clicker was paired with the former US2-Diff event. Over all of Test 2, D suppressed head-jerk behavior more in Group Down than in Group High, $t(14) = 2.61$, and more in Group High than in Group Up, $t(14) = 2.80$. That pattern of data implies that Phase 2 training made D inhibitory with respect to US2-Diff in Group Down and excitatory in Group Up. There were no reliable differences among the groups in the suppressive power of S. The left side of Figure 7 shows the discrimination difference scores for the rats in which the clicker was paired with the former US1. There were few reliable differences among the cues and/or groups. Although neither group differed reliably from controls, the S cue suppressed head-jerk behavior more in Group Down than in Group Up, $t(14) = 3.91$, which implies that Phase 2 treatment produced some difference in either excitatory or inhibitory powers of S, relative to US2-Same, in those groups.

Discussion

Experiment 3 replicated the major data patterns of Experiments 1 and 2 and added information about the acquisition of conditioned inhibition after downshifts in reinforcer num-

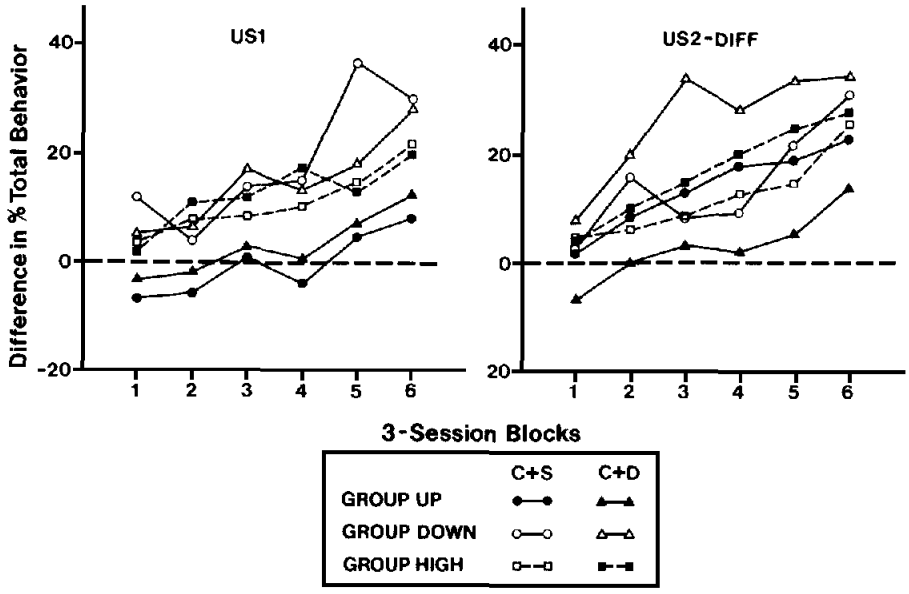

Figure 7. Discriminated head-jerk behavior during the inhibitory savings test sessions of Experiment 3. (Each point represents the mean difference between the level of head jerk that occurred on excitor-alone trials and the level that occurred on inhibitory compound trials. Thus, values greater than zero indicate inhibition to the added, test cue, and values less than zero reflect excitation. The left panel shows responding of the rats that had the clicker paired with US1 in the savings test, and the right panel shows responding of the subjects that received clicker–US2 pairings. The curves labeled C+S show discriminated performance with the compound of clicker and the *S*ame cue from Test 1, and those labeled C+D show discriminated performance that involved the compound of clicker and the *Diff*[erent] cue from Test 1.)

ber. Novel cues that accompanied upshifts in the reinforcer acquired excitatory powers, especially if US1→US2-Diff sequences were used. Cues that accompanied downshifts in the reinforcer acquired net excitatory powers if US1→US2-Same sequences were used but net inhibitory powers if the downshift was from a heterogeneous US1→US2-Diff sequence. Thus, the differential effects of heterogeneous and homogeneous up- and downshifts found in these experiments seem attributable to the differential influence of US2 parameters on US2's association-modulating and association-formation functions.

Experiment 4

Why should the salience of US2 omission affect the acquisition of inhibitory CS–US2 associations more than the acquisition of excitatory CS–US1 associations? Hall (personal communication, February 1984) suggested that the temporal gradient of association formation is steeper than that of modulation. That is, the band of time in which a US2 (or its omission) may enter into associations with the CS is narrower than the interval over which those events may enhance associations between CS and US1.

Figure 8 shows hypothetical powers of associative and modulatory powers of the omission of US2-Same and US2-Diff events, after training with US1–US2 intervals of varying length. The top panel shows separate curves for inhibitory CS–US2 strength and excitatory modulatory power, and the bottom panel shows net excitation (obtained by subtracting the inhibitory gradient from the excitatory one). For example, a US2-Same omitted at point X can still substantially affect CS–US1 associations but can support only minimal inhibitory association with the CS. Consequently, net excitatory conditioning (unblocking) is observed when the US1→US2-Same sequence of interval X is downshifted to US1 alone. Conversely, at time 0 (US2-Same and US1 coincident), the inhibitory powers of US2-Same omission outweigh its excitatory influences on CS–US1 association, and the added CS would become a net inhibitor. It is worth noting that the published instances of downshifts in reinforcer magnitude that produced inhibition (e.g., Cotton, et al., 1982; Mackintosh & Cotton, 1985; Wagner et al. 1980) all contrasted a large single US with a smaller single US—that is, presented the downshift at time 0,—and most published instances of excitatory conditioning with downshifts involved the omission of another, subsequent event–that is, one presented at time X. By similar logic, if increasing the salience of US2, by making it different from US1, shifts those gradients to the right (dotted curves), then the omission of a more salient US2-Diff may generate net inhibition over longer US1–US2 intervals than with omission of US-Same. Likewise, variations in salience of the omitted US2 would have proportionally larger effects on inhibitory conditioning than on excitatory modulation, at any point at which the gradient of inhibitory conditioning was steeper than that of modulatory powers.

Consequently, at some CS (or US1)–US2 intervals (point X on Figure 8, for example), omitting US2-Same may encourage net excitatory CS–US1 association, but omitting

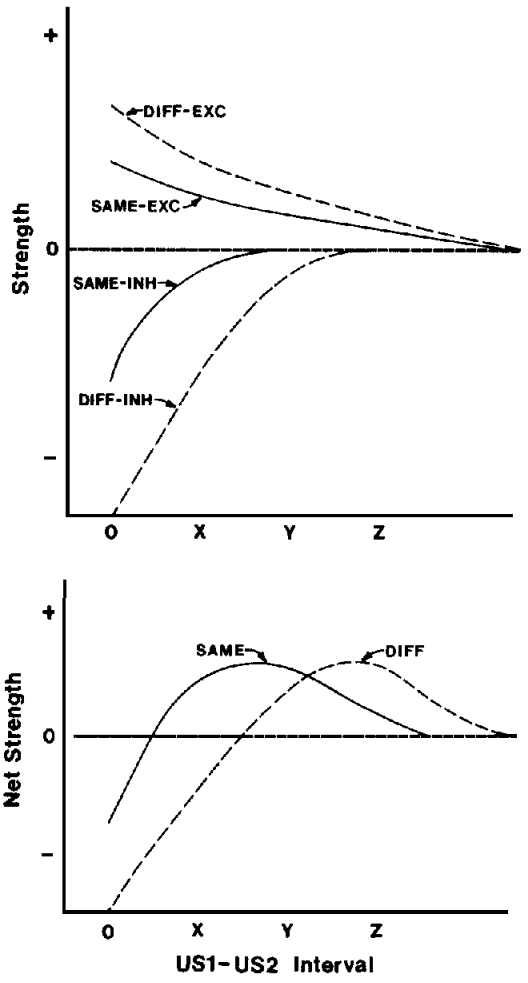

Figure 8. Top panel: Hypothetical interval functions for excitatory modulatory (EXC) and inhibitory associative (INH) powers of an omitted US2, when that US2 event was either qualitatively similar to (SAME) or different from (DIFF) US1. Bottom panel: Hypothetical temporal gradients of net associative strength of a novel cue paired with omission of an anticipated US2 that was either qualitatively similar to (SAME) or different from (DIFF) US1. (In both panels, the 0 interval refers to a 0-s interval; the significance of the intervals labeled X, Y, and Z is explained in the text.)

US2-Diff may encourage net inhibitory CS–US2 association, as in Experiment 3. However, at other intervals, those effects may differ. For example, with interval 0, omission of either US2 would generate net inhibition. Conversely, at interval Y, both omissions would encourage excitatory learning. And at interval Z the omission of US2-Diff would generate *more* excitatory CS–US1 association than the omission of US2-Same. To test these predictions, in Experiment 4 I examined the effects of downshifts to a single US1 from heterogeneous and homogeneous US1→US2 sequences of various US1→US2 intervals.

Rats received training with one visual CS paired with a heterogeneous US1→US2-Diff sequence and another visual CS paired with a homogeneous US1→US2-Same sequence. The interval between US1 and US2 in both sequences varied between 0 and 60 s across groups. Then, a different auditory cue was compounded with each visual cue, and the compounds both followed by US1 alone in each group. After the excitatory powers of the two auditory cues were examined in an extinction test, the inhibitory powers of those cues were assessed in a retardation test.

Method

Subjects and apparatus. The subjects were 24 male and 24 female, experimentally naive Sprague-Dawley rats. They were bred from Charles River stock in the Duke University psychology department and were 120 days old at the beginning of the experiment. They were maintained as in the previous experiments, except that experimental sessions were conducted between 6:00 a.m. and 3:00 p.m.

Procedure. All rats first received food cup training, as in Experiments 2 and 3. Experiment 4 was conducted in one replication.

In Phase 1, all subjects received four pairings of one 10-s visual cue (A) with a US1→US2-Same sequence, and four pairings of another 10-s visual cue (B) with a US1→US2-Diff sequence in each of eighteen 90-min sessions. Cues A and B were a 10-s intermittent (3 hz) illumination of the houselight and a 10-s constant illumination of the panelight, fully counterbalanced. For all subjects, US1 was the delivery of one 45-mg food pellet, US2-Same was the delivery of two 45-mg food pellets, and US2-Diff was the delivery of 0.3 ml of 0.2-M sucrose solution. The groups differed in the intervals between US1 and US2; the intervals between US1 and US2-Diff and between US1 and US2-Same were identical in all five groups. In Groups 0 and C, those intervals were 0 s—that is, US1 and US2 were delivered simultaneously. In Groups 5, 10, and 30, those intervals were 5, 10, and 30 s, respectively.

In Phase 2, all subjects received 10 compound conditioning sessions. In each of those sessions, all rats, except those in Group C, received four presentations of the 10-s compound AS followed by a single 45-mg food pellets, and four pairings of a 10-s BD compound with one 45-mg food pellet. Auditory cues S and D were a white noise and a 1500-hz tone, fully counterbalanced. Thus, all of the rats, except those in Group C, experienced downshifts from a homogeneous sequence after AS, and downshifts from a heterogeneous sequence after BD. The rats in Group C also received AS and BD compound stimuli in this phase, but the reinforcers were unchanged from Phase 1. That is, A was followed by the simultaneous delivery of pellets, and B was followed by the simultaneous delivery of 1 pellet and 0.3 ml of sucrose solution.

In Test 1, the response-evoking powers of the added auditory cues were assessed; four nonreinforced S and four nonreinforced D presentations occurred in a single 90-min session. Next, the rats received two more sessions, identical to Test 1, which were designed to extinguish responding evoked by S and D. Test 2 used a retardation test to determine if inhibitory associations had been formed between D and US2-Diff and between S and US2-Same, the events that were omitted after BD and AS trials in Phase 2. In each of five 90-min sessions, all subjects received four presentations of S, each paired with the delivery of two 45-mg food pellets (US2-Same), and four presentations of D, each paired with the delivery of 0.3 ml of sucrose (US2-Diff). Conditioned inhibition in Groups 0, 5, 10, 30, and 60 was indexed by slower acquisition of responding to S and/or D than observed in Group C.

Results

Phase 1. Conditioning in Phase 1 proceeded as in the previous experiments. Over the final two sessions, there were

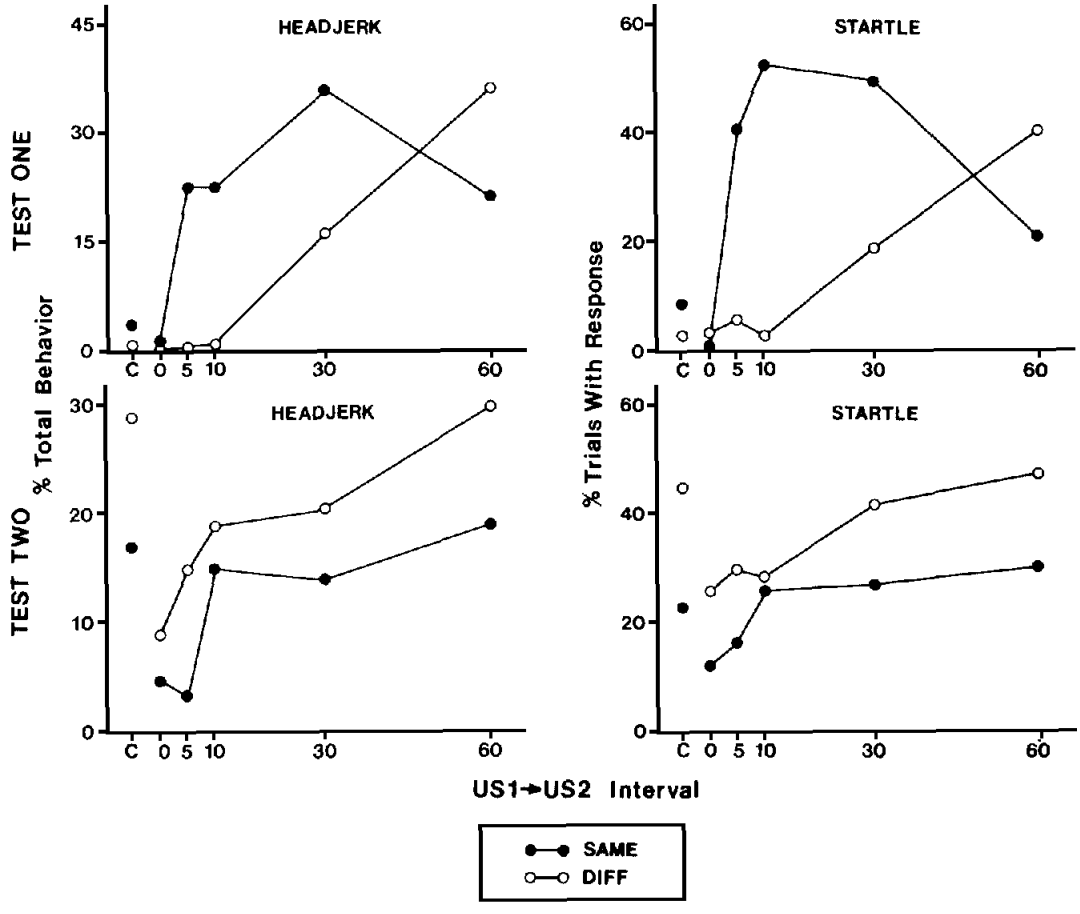

Figure 9. Head-jerk and startle behaviors during the tests in Experiment 4. (Test 1 [top panels] measured net excitation to the target cues, and Test 2 [bottom panels] indexed inhibition by measuring the retardation of acquisition of excitation to those cues. The curves labeled SAME show performance to the cue that had been paired with the omission of a US2 that was similar to US1, and the curves labeled DIFF[erent] show performance to the cue that had accompanied the omission of a qualitatively different US2. Groups, which differed in Phase 1 US1–US2 interval, are arrayed along the abscissas. Group C received a 0-s US1–US2 interval in Phase 1, but no downshifts in Phase 2; the other groups were named by their US1–US2 intervals. In the top panels, net excitation [unblocking] is indicated by more conditioned responding than found in Group C. In the bottom panels, inhibition is indicated by less conditioned responding over the course of all the retardation test sessions than found in Group C. All entries are means.)

no reliable differences in the frequency of rear behavior among either stimuli or groups (range: 14%–24%). US1-directed behavior (magazine) occurred at similar levels during both visual stimuli in Groups 5, 10, 30, and 60 and during the same cue in Groups 0 and C (range: 46%–54%) but was less frequent during the different cue in Groups 0 (32%) and C (25%). Those differences are attributable to the occurrence, in Groups 0 and C, of US2-directed behavior (cup) during the visual cue paired with the food + sucrose reinforcer (24% and 15%, respectively). US2-behavior comprised 10% of the behavior during the same cue in Group 0, 5% during that cue in Group C, and less than 5% of the behavior during either cues in the other groups.

Group × Stimulus ANOVAs showed no reliable effects or interaction for rear behavior (Fs < 1) but significant interactions for magazine and cup behaviors, $F(5, 42) > 4.20$. In Groups 0 and C (combined), cup behavior was more frequent and magazine behavior less frequent during the Diff cue than during the Same cue, ts(14) ≥ 2.79.

Phase 2. In Phase 2, head-jerk and startle behaviors were acquired to the AS compound in Groups 5 (25% and 40%, respectively, over the final two sessions), 10 (31% and 60%), 30 (41% and 50%), and 60 (15% and 21%), and to the BD compound in Groups 30 (7% and 20%) and 60 (29% and 50%). Head-jerk behavior comprised less than 5% of the total behavior, and startle occurred on fewer than 10% of the trials for any of the other compounds in Phase 2. The data trends in this phase were similar to those of Test 1; in the interests of economy, only analyses of Test 1 data are presented here.

Test 1. Figure 9 shows startle and head-jerk behavior to the Same and Diff cues in the first session of Test 1 in the six groups. In all groups, at least 95% of the head-jerk behavior

was US1-directed—that is, oriented toward the recessed food magazine. Group × Cue ANOVAs revealed significant interactions, $Fs(5, 42) > 7.87$. The Same cue evoked reliably more head jerk behavior in Groups 5, 10, 30, and 60 than in the unshifted control, Group C, $ts(14) > 2.32$, but the Diff cue evoked significantly more of that behavior only in Groups 30 and 60, $ts(14) > 2.63$. Startle behavior was reliably greater than control levels in Groups 10 and 30 during the Same cue, $ts(14) > 2.22$, and in Group 60 during the Diff cue, $t(14) = 2.15$. The Same cue evoked more of both behaviors than the Diff cue in Groups 5, 10, and 30, $ts(7) > 2.57$, but the Diff cue evoked more in Group 60, $ts(7) > 3.08$. Neither cue evoked more conditioned behavior in Group 0 than in Group C.

Retardation test. The bottom panels of Figure 9 show head-jerk (left panel) and startle (right panel) behaviors averaged over the five retardation test sessions. Comparisons of those overall means showed that relative to controls (Group C), acquisition of both behaviors was significantly retarded to the Same cue in Group 0, $ts(14) > 2.63$, and to the Diff cue in Groups 0, 5, and 10, $ts(14) > 2.19$. In addition, the acquisition of head-jerk behavior was reliably slowed to the Same cue in Group 5, $t(14) = 2.50$, and to the Diff cue in Group 30, $t(14) = 2.16$. Separate Groups × Sessions ANOVAs showed reliable effects of both factors and their interaction, for both the Same and Different cues. One-way analyses of performance during the first session of the retardation test showed no reliable effects of groups ($Fs < 1$). Thus, the differences in overall retardation test performance are not readily attributable to different starting points (recall that the second and third sessions of Test 1 were intended to extinguish responding to S and D, prior to the retardation test.)

Discussion

Omission of US2 when a novel cue was added to a stimulus that had been previously paired with a US1→US2 sequence produced both excitatory and inhibitory conditioning of the added cue. If US2 was qualitatively similar to US1, the added cue acquired inhibitory powers when the US1→US2 interval was virtually zero, but net excitatory strength when 5 s or more intervened. If US2 was different from US1, the added cue acquired inhibitory powers when the US1→US2 interval was 10 s or less and excitation when that interval was 30 s or 60 s.

The excitation acquired in Experiment 4 was most likely the consequence of CS–US1 association, because over 95% of the conditioned behavior was oriented toward the site of US1 delivery. Thus, there was no evidence that CS–US2 associations are formed with downshifts. Holland (1981) argued that under some circumstances, a CS may acquire associations with an absent US if it accompanies a cue that has been paired with that US.

The pattern of data obtained in Experiment 4 is consistent with the claims (described earlier) that the temporal gradient of US2 omission's ability to generate inhibitory CS–US2 association is steeper than that of its ability to enhance CS–US1 excitatory association and that those gradients are extended with the omission of a US2 that is qualitatively different from US1. The forms of the response curves in the top panels of Figure 9 are compatible with the hypothetical net curves shown in the lower panel of Figure 8, and the inhibitory curves of the bottom panels of Figure 9 are consistent with the hypothetical inhibitory gradients shown in the top panel of Figure 8. For example, point X in Figure 8 might well refer to the 5- or 10-s interval in Figure 9, point Y to the 30-s interval, and point Z to the 60-s interval.

The curves in Figure 8 were constructed with the simple assumption that the gradients are simply shifted to the right for US2-Diff events, relative to US-Same events. However, another transformation that preserves the greater slope of the associative–inhibitory function than the facilitory–excitatory function may be more appropriate. That determination awaits a detailed quantitative analyses of these and related data.

Kremer et al. (1980) also found greater conditioning in a downshift procedure if the original US1–US2 interval had been 30 s rather than 1 or 3 s, but they attributed their finding to variations in contextual conditioning. They argued that in the first phase of an unblocking experiment, contextual cues compete with the explicit CS for association with US1, as suggested by Rescorla and Wagner (1972). Omission of US2 when the novel target cue is introduced results in partial extinction of the contextual cues, permitting the association of the target with US1. Thus, the greater the contextual conditioning in Phase 1, the more opportunity for the target to acquire conditioning in Phase 2. With longer US1–US2 intervals, US2 is less effectively signaled and hence may produce more contextual conditioning.

It is unlikely that such a mechanism played an important part in the experiments reported here. First, Kremer et al. (1980) used an intense 2-mA shock US known to produce substantial contextual conditioning, whereas in these experiments, the small food and sucrose USs typically produce little evidence of contextual conditioning (e.g., Holland, 1984b). Second, if the US1–US2 interval acted by causing variations in contextual conditioning, then both target cues in each group should be similarly affected. But conditioning of the Same and Different target cues did not covary. Finally, Kremer et al.'s (1980) mechanism would not anticipate unblocking with both upshifts and downshifts at any given interval: If omission of a second US permits partial extinction of the context, allowing the added cue to gain excitation, then addition of that US would further condition the context, producing losses in conditioning of the added cue.

Finally, it is of interest to note evidence that the added target cue may simultaneously possess both excitatory and inhibitory properties. In Experiment 4, both the Diff cue in Group 30 and the Same cue in Group 5 showed reliable excitation in Test 1 and marginal inhibition in Test 2. Similarly, the Same cue in Group Down of Experiment 3 (equivalent to Group 5 of Experiment 4) showed reliable excitation in Test 1 and marginal inhibition in Test 2. Holland (1984a) and Schachtman, Brown, Gordon, Catterson, and Miller (1987) have noted other examples of cues simultaneously possessing excitatory and inhibitory powers.

General Discussion

These experiments examined the topography (orientation) of conditioned behavior and the sensitivity of that behavior to selective satiation to help clarify what is learned in unblock-

ing procedures. Upshifts in a reinforcer sequence, from US1 to US1→US2, can both enhance excitatory association between the target cue and US1 and establish excitatory association between the target and US2. Downshifts in the reinforcer sequence, from US1→US2 to US1 alone, can both enhance excitatory associations between the target and US1 and establish *inhibitory* associations between the target and US2.

Thus, omitted or presented US2 events have both a direct effect on learned responding (by participating in associations with the CS) and an indirect effect (by potentiating associations between the CS and US1). Because those effects are competitive in the case of US2 omission, the outcome of a particular reinforcer downshift procedure depends on the relative weight of those two processes. These experiments identified two variables—the US1–US2 interval and US1–US2 similarity—that seem to affect those processes differentially.

Experiment 4 revealed that downshift procedures generated net inhibitors with short US1–US2 intervals but net excitors with longer US1–US2 intervals. This outcome implies that the temporal gradient of the excitatory–facilitory function is broader than that of the inhibitory–associative function under the circumstances tested here. Furthermore, both gradients were broader for US2-Diff events than for US2-Same events.

Why might the omission of US2 produce broader gradients when US2 differs qualitatively from US1? Although there may be many ways that differing US2s especially engage both associative and facilitatory processes, it seems parsimonious to consider US2-Diff events within US1–US2 sequences simply as more salient than US2-Same events in those sequences. That assumption is shared by theories like Wagner's (1978, 1981), which posit that events not already primed into an active memory state are more effectively processed than events already in that state (as a result of prior presentation), and is supported by substantial data (e.g., Terry, 1976; Wagner, 1978; Whitlow, 1975).

Two implications of that assumption are especially interesting. First, and most straightforward, if qualitatively different US2 events are viewed as generating broader gradients because they are effectively more salient, then similarly broadened gradients should result with qualitatively similar US2 events that are more salient in their own right, that is, of greater magnitude, quantity, or intensity. Thus, the omission of larger US2 events should produce less net excitation than the omission of smaller US2 events at brief US1–US2 intervals but more net excitation at longer intervals, as occurred in Experiment 4 with different and same US2s.

Second, if the salience of qualitatively similar US2 events is reduced because US1 presentation has primed those events into an active memory state at the time of US2 delivery, then manipulations that remove them from that state before US2 delivery should enhance the effectiveness of US2-Same events. For example, presentation of a distractor event in the US1–US2 interval that displaces US1 might enhance processing of US2-Same. Consequently, in the case of upshifts, that distractor might enhance unblocking, and with downshifts it would reduce net excitation at short intervals and increase it at long intervals.

I must point out that although the experiments reported here implicate a modulatory function of surprise, they shed little light on the nature of that process. Does the surprising presentation or omission of US2 enhance CS–US1 association by promoting processing of the CS, US1, or the CS–US1 episode as a whole or by some other mechanism? Although Holland (1985b) and Mackintosh and Turner (1971) have presented data that implicate alterations in CS processing in these procedures, other modulatory functions cannot be ruled out.

Regardless of the nature of the modulatory process, the experiments reported here help resolve many of the apparent inconsistencies in the unblocking literature. The various observations of excitation, no learning, and inhibition in unblocking experiments may simply reflect the differential sensitivity of the associative and modulatory processes identified here to certain parametric variations.

Last, it is worth noting that unblocking experiments bear at least a superficial similarity to instrumental incentive contrast experiments (see Flaherty, 1982, for a recent review). Subjects are trained with either large or small rewards in the first phase, and then the rewards are either shifted to the other reward value or maintained in the second phase. In the second phase, subjects often respond more with the large reward after an upshift from the small reward than if they had received the large reward in both phases (positive contrast effect), and they respond less with a small reward if they had received downshifts from the large reward than if they had received the small reward in both phases (negative contrast effect). These contrast effects might be considered analogous to my observations of greater excitation to an added cue after upshifts (relative to "high" controls), and inhibition (in some circumstances) to the added cue after downshifts (relative to "low" controls).

The analogy may be tenuous on many counts. First, although typically the negative contrast effect is robust and the positive contrast effect more elusive (Flaherty, 1982), in the present experiments, inhibition after downshifts was observed only under certain conditions (indeed, *greater excitation* after downshifts was the more frequent finding here), and greater excitation with upshifts was substantial in all conditions. Second, although Experiments 1, 3, and 4 could be regarded as analogous to a standard successive contrast experiment (in which subjects receive one reward value in Phase 1 and another in Phase 2), Experiment 2 combines the features of successive contrast experiments with those of simultaneous contrast experiments (in which subjects receive both reward values in the same sessions).

Most important, in unblocking experiments, the effects of US shifts on learning to a cue *added at the time of the shift* are examined, whereas in contrast experiments, the effects of the shift on already established behavior are examined. It might be argued that the added-cue assessment reveals the effect of the shift more directly, because the added cue has no previously established response tendencies. It would be interesting to adapt the added cue technique to instrumental incentive contrast procedures.

In this regard, it is worth noting that Experiment 2 contained a Pavlovian analogue of the typical incentive contrast assessment, as well as the added cue assessment. After Phase 1 training with two different visual cues, each paired with a different US (US1 or US1→US2 sequence), a novel auditory

cue was added to only one of the visual cues, and the US was either shifted or not after *both* compound and visual element-alone trials. Thus, examination of responding to the element alone in Phase 2 after shifts or no shifts in the US is comparable to the usual incentive contrast test. A reliable negative contrast effect was obtained; that is, subjects responded less to the visual cue paired with the single US1 if that cue had previously been paired with the US1→US2 sequence than if it had always been paired with the single US1. Conversely, no positive contrast effect was observed: Phase 2 responding to the visual element-alone cue paired with the US1→US2 sequence was identical regardless of whether that cue had been previously paired with the single US1 or US1→US2 sequence.

It is tempting to contrast, after upshifts, the lack of a positive contrast effect during the visual element-alone cue with the substantial acquisition of excitation to the added auditory cue, and after downshifts, the occurrence of a negative contrast effect during the element-alone cue with the acquisition of *excitation*, rather than inhibition, to the added cue. Although these contrasts certainly suggest that unblocking and incentive contrast effects are at least not positively correlated, caution is in order. First, although unblocking has been studied with instrumental procedures (e.g., Dickinson & Mackintosh, 1979), little is known about incentive contrast in Pavlovian procedures. Second, it is conceivable that the different outcomes of the added cue and element-alone assessments in Experiment 2 were related to the different behavioral measures involved: The conditioned response evoked by the visual element-alone cue in Experiment 2, US1-goal responding, was different from the CR evoked by the added auditory cue, head jerk, and startle behaviors.

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Received June 23, 1987
Revision received September 9, 1987
Accepted September 10, 1987 ■