Control of conditional discrimination performance by CS-evoked event representations

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The ability of visual CSs previously paired with flavored substances to substitute for those substances as conditional discriminative cues was examined in two Pavlovian appetitive conditioning experiments using rat subjects. In Experiment 1, a visual stimulus was first paired with the delivery of a sucrose solution. Then the rats were trained in conditional discrimination tasks in which sucrose delivery alone served as a conditional cue signaling whether or not a subsequent tone would be reinforced with food pellets. Subjects rapidly acquired discriminative performance to the tones, especially in a feature-negative condition in which sucrose delivery signaled when the tone would not be reinforced. In a subsequent test in which neither food nor sucrose was delivered, presentation of the visual CS also controlled discriminative performance to subsequently presented tones. Experiment 2 showed the ability of a visual CS to substitute for a flavored substance as a conditional cue to be highly stimulus specific. Experiment 2 also showed that a flavored substance was less effective as a conditional cue when it was made to be expected by preceding it with a previously associated visual signal than when it was made to be surprising by preceding it with a visual stimulus signaling another flavored liquid. These results indicate that CS-evoked representations of events can substitute for those events themselves in the control of previously established conditional discrimination performance.

Many recent theories of Pavlovian conditioning agree that conditioned responding is mediated by a representation or memory of the unconditioned stimulus (US) (e.g., Dickinson & Mackintosh, 1978; Pearce & Hall, 1980; Rescorla, 1979). Typically, it is claimed that conditioned responding develops when the conditioned stimulus (CS) comes to evoke a US representation that prior to conditioning was evoked only by the US itself. Many theorists have further assumed that activations of such a US representation by either the US itself or by a CS are equivalent in many respects. For example, Konorski (1967) attributed the frequently observed similarity of conditioned responses (CRs) and unconditioned responses (URs) to the fact that both responses are produced by activation of the same US representation. Likewise, Wagner (1978) and his colleagues (e.g., Terry, 1976) have noted that interference effects attributed to priming of the US representation into a short-term memory system occur whether that representation was primed by the US itself or was retrieved by a CS previously associated with the US.

Recently, we have claimed that a representation of an event retrieved from memory by a previously associated stimulus can substitute for the event itself

in the formation of new associations involving that event. Holland (1981) established food aversions in rats by inducing illness immediately after the evocation of a representation of a particular food substance (by a previously associated tone CS) in the absence of food itself. Similarly, Forbes and Holland (Note 1) extinguished a flavor aversion originally established by flavor-illness pairings by repeatedly presenting without consequences a tone that had been previously paired with that flavor.

The experiments reported here examined the ability of an event representation retrieved from memory to substitute for the event itself in a function previously acquired by that event itself—specifically, the ability to serve as a conditional discriminative cue. Rat subjects were trained using a conditional discrimination procedure termed the “preparatory-releaser” technique (e.g., Bottjer & Hearst, 1979; Terry & Wagner, 1975). Delivery of a flavored liquid “preparatory” stimulus indicated whether or not a subsequently presented “releaser” tone would be followed by the delivery of food pellets. After subjects mastered this conditional discrimination, showing general activity responding to the tone only on reinforced trials, the ability of a visual CS previously paired with the flavored liquid to substitute for that liquid in modulating performance to the tone was assessed. Experiment 1 showed that an evoked representation of a flavored liquid could in fact substitute for that liquid itself as a conditional (preparatory) cue. Experiment 2 examined the stimulus specificity

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of such substitution. Experiment 2 also compared the ability of "surprising" and "expected" flavor stimuli to act as conditional cues (cf. Terry & Wagner, 1975).

EXPERIMENT 1

Two groups of rats first received discrimination training designed to endow one visual stimulus with the ability to evoke a representation of a liquid sucrose reinforcer but to leave a second visual stimulus relatively neutral. Then the rats were trained on one of two conditional "preparatory-releaser" discriminations. In the "feature-positive" (Jenkins & Sainsbury, 1969) group, the delivery of sucrose indicated that a tone presented 20 sec later would be reinforced with food pellets; tones not preceded by sucrose delivery were not reinforced. In the "feature-negative" group, tones preceded by sucrose delivery were not reinforced, but those presented alone were reinforced. Finally, all rats received a test session in which the tones were preceded by the visual stimulus that presumably evoked a representation of sucrose, the neutral visual stimulus, or no stimulus.

Method

Subjects and Apparatus. The subjects were 16 experimentally naive Sprague-Dawley rats, about 130 days old at the beginning of the experiment. Half of the subjects in each group were male, and half were female. They were maintained at 80% of their ad-lib body weights by limiting their access to food.

The experimental chambers consisted of eight identical boxes, $22.9 \times 20.3 \times 20.3$ cm. Each chamber had a recessed food magazine fitted with a neon glow tube in the center of the front wall. A 6-W jeweled signal light was located 9 cm above the food magazine. A liquid cup protruding 3.7 cm into the chamber was mounted on the back wall. The floor of the chamber was composed of .48-cm stainless steel rods spaced 1.9 cm apart. The two end walls were aluminum; the side walls and top were clear acrylic plastic. Each chamber rested on a stabilimeter-type activity-measuring device consisting of two horizontal acrylic sheets (separated by three self-centering ball-bearing assemblies) and a transducer mounted on the top sheet. The transducer consisted of a stainless steel weight suspended within a circular hole in a stainless steel plate. The weight and edge of the hole served as contacts in an electronic counting circuit. Movement of the rat caused the top acrylic sheet to roll slightly, forcing the weight to strike the edges of the hole, making and breaking the circuit. Each stabilimeter-chamber assembly was enclosed in a light- and sound-attenuating closet. A 6-W houselight used only as a CS was mounted on the inside wall of each closet, about 10 cm above and in front of the experimental chamber. A speaker for delivering auditory stimuli was mounted next to each houselight. Continuous masking noise was provided by a ventilation fan in each chamber.

Procedure. All rats first received discrimination training designed to endow the houselight with the ability to evoke a representation of a sucrose reinforcer but to leave the signal light relatively neutral. In each of 12 75-min sessions, the rats received four 10-sec presentations of the flashing (3/sec) houselight followed by delivery of .5 ml 8% (weight/volume) sucrose to the liquid cup, and four nonreinforced 10-sec presentations of the steady signal light. The neon lamp in the recessed food magazine was not illuminated in this phase.

Next, the rats received 10 sessions of conditional discrimination training. In each 75-min session, all rats received four serial com-

pound trials consisting of the delivery of .5 ml 8% sucrose to the liquid cup (the conditional cue) followed 20 sec later by a 10-sec 1,500-Hz tone, and four 10-sec 1,500-Hz tone-alone trials. In Group FP (feature-positive), two 45-mg Noyes pellets were delivered coincident with tone termination on sucrose-tone compound trials only; in Group FN (feature-negative), only tone-alone trials were reinforced with food pellets. All food pellets were delivered to the recessed food cup, which was illuminated during this phase and in subsequent testing.

Finally, all rats received a single 75-min test session in which the ability of the flashing houselight to substitute for sucrose delivery as the conditional cue was examined. Three presentations of each of three types of trials were administered: on one type of trial (A), a 10-sec flashing houselight was followed by a 10-sec trace interval and then the 10-sec tone; on a second kind of trial (B), a 10-sec steady signal light was followed by a 10-sec trace interval and then the 10-sec tone; and a third type of trial (C) consisted of the 10-sec tone alone. The order of trial presentation was CABABCBA for all rats. No sucrose or food pellets were delivered in testing.

Activity counts during all stimulus presentations and 20-sec intervals preceding stimulus presentations were recorded throughout the experiment. The level of statistical significance adopted was $p < .05$.

Results

As in previous experiments (e.g., Holland, 1977), little activity was generated by the flashing houselight paired with food in the first, light discrimination phase. Over the last two sessions of that phase, the median activity counts per minute were 17.6 during the houselight, 13.2 during the signal light, and 16.6 during pre-CS periods.

The left portion of Figure 1 shows responding to the reinforced (T+) and nonreinforced (T-) tone stimuli in both groups during training of the conditional discriminations. The discriminations were readily acquired; over all training sessions, responding to T+ was greater than responding to T- in both Group FP (Wilcoxon $T = 3.5$) and Group FN ($T = 0$). Thus, sucrose delivery acquired the ability to serve as a conditional cue signaling the availability or non-availability of food after subsequent tone presentations. There was some evidence that the feature-negative discrimination (Group FN) was acquired more readily. Although T+ responding did not differ reliably between Groups FP and FN, T- responding was significantly greater in Group FP than in Group FN (Mann-Whitney $U = 13$). Furthermore, discrimination scores obtained by subtracting individual rats' T- responding from their T+ responding were significantly greater in Group FN ($U = 6$).

Evidence for learning the conditional discrimination was confined to responding during the tones. The conditional cue (sucrose delivery) itself evoked no more activity when it was followed by food delivery (Group FP) than when it occurred only on nonreinforced trials (Group FN): over the course of conditional discrimination training, median activity during the 20-sec interval after sucrose delivery but preceding tone presentation was 27.8 counts per min in Group FP and 33 counts per min in Group FN

Figure 1. Responding during discrimination training in Experiment 1. The left panel shows responding during the reinforced (T+) and nonreinforced (T-) tones in Group FP (feature-positive) and Group FN (feature-negative). The right panel shows difference scores calculated by subtracting response rates prior to T+ or T- from response rates during T+ or T-, respectively.

($U=28$). Sucrose delivery apparently did increase activity above baseline levels, however: there was marginally ($T_s < 6$, $p_s < .10$) more activity during the 20 sec after sucrose presentation than during comparable 20-sec periods prior to tone-alone presentations in both Group FP (19.5 counts per min prior to tone-alone) and Group FN (16.9 counts per min).

Responding during T+ and T- presentations may to some extent have reflected this differential pretone responding on tone-alone and sucrose-tone trials. To minimize the influence of differential pretone activity rates on our assessment of conditional discrimination performance, we computed during tone - pretone activity the scores for both T+ and T- presentations (right portion of Figure 1). Comparison of T+ and T- trial responding using this measure also suggested that the rats in Group FP ($T=6$, $p < .10$) and Group FN ($T=0$) acquired the conditional discrimination. Furthermore, significantly less responding to T- ($U=7$) and marginally more responding to T+ ($U=16$, $p < .10$) occurred in Group FN than in Group FP, indicating that the feature-negative discrimination was more readily acquired than the feature-positive discrimination.

The primary data of Experiment 1 were the results of the test in which the ability of the flashing houselight to substitute for sucrose delivery as a conditional cue was examined. The left portion of Table 1 shows responding to the tone after presentation of the houselight (previously paired with sucrose), the signal light (not previously paired with sucrose), or no event. Friedman analyses of variance showed that responding to the tone differed on the three types of trials ($\chi^2_s \leq 87.56$). Paired comparisons showed that

in Group FP, in which sucrose indicated that the tone was to be reinforced, the tone evoked significantly more activity when it was preceded by the houselight than when it was preceded by either no event ($T=1$) or the signal light ($T=4.5$). Conversely, in Group FN, responding to the tone was significantly lower when it was preceded by the houselight than when it was preceded by the signal light ($T=0$) or no event ($T=3.5$). Thus, the houselight CS alone substituted for sucrose delivery both as a signal to respond to a subsequent tone (Group FP) and as a signal to withhold responding to a subsequent tone (Group FN).

The center portion of Table 1 shows response rates during the 20-sec interval preceding tone presentations. In Group FP, there were no reliable differences regardless of whether that interval had included the 10-sec houselight, the 10-sec signal light, or no explicit stimulus. But in Group FN, pretone rates were

Table 1
Median Activity Counts per Minute in Experiment 1 Testing

	Group					
	During Tone		Pretone		During-Pretone	
	FP	FN	FP	FN	FP	FN
After CS+	54	71	33	65	21	6
After CS-	35	86	31	50	4	36
After ϕ	15	87	26	22	-11	65

Note—CS+ = flashing houselight previously paired with sucrose, CS- = steady panel light previously not paired with sucrose, and ϕ = no event. "Pretone" rates indicate responding during the 20-sec interval immediately prior to tone presentation; that interval occurred immediately after CS termination on CS+ and CS- trials.

higher if that interval included the houselight ($T=4$, $p < .05$) and marginally higher if it included the signal light ($T=6$, $p < .10$) than if it included no explicit stimulus. We have no ready explanation for this variation in pre-CS rates over the various kinds of trials in Group FN but not in Group FP. It should be noted, however, that the elevated pretone rates in Group FN tend to obscure the ability of the houselight to substitute for sucrose as a signal to withhold responding in that group. The right portion of Table 1 shows difference scores obtained by subtracting pretone activity rates from during-tone activity rates. Those data show more clearly the differential responding to the tone depending on whether or not it was preceded by a signal for sucrose in Group FN. In both groups, the difference scores on houselight-tone trials differed reliably from those on the other two types of trials ($T_s < 3.5$); the apparent differences between such difference scores on signal light-tone and tone-alone trials (perhaps suggesting generalization between the two visual stimuli) were not reliable ($T_s > 9$).

Discussion

Rats quickly solved discriminations in which sucrose delivery indicated whether or not a subsequent tone would be reinforced with food. Unlike in considerable previous research (e.g., Hearst, 1978), discrimination performance in the feature-negative (FN) group was superior to that in the feature-positive (FP) group. This unusual outcome encouraged us to observe the behavior of the rats through "fish-eye" viewers mounted in the walls of the sound-attenuating closets during the last four sessions of discrimination training. These observations showed that one important component of the activity response, startle responding to the tone (defined as a sudden change in position, Holland, 1977), occurred on a median of 81% of the reinforced tone-alone trials in Group FN but on only 12% of the reinforced sucrose-tone trials in Group FP. This finding is consistent with other data collected in our laboratory (Holland & Ross, 1981) showing that conditioned tones signaled by a visual stimulus (as in a light-tone serial compound) evoke substantially less startle than do unsignaled tones. Thus, the "general activity" responding to the reinforced tones in the two groups may in fact reflect quite different detailed behaviors; measurement of other components of general activity such as the head jerk behavior described by Holland (1977) might reveal a feature-positive superiority, as has typically been observed in other preparations. Unfortunately, the "fish-eye" viewers produced too much distortion to reliably distinguish behaviors other than startle in this experiment.

More important for our present concern, in testing a visual CS previously paired with sucrose delivery substituted for the sucrose itself in controlling be-

havior to a subsequently presented tone. This outcome is consistent with the notion that the visual CS evoked an internal representation of the sucrose delivery and that such a CS-evoked or "retrieval-primed" (Wagner, 1978) representation was similar enough to the representation evoked or primed by the sucrose itself to possess similar conditional cue functions.

Terry and Wagner (1975) noted a similar phenomenon. In their experiment, rabbits received feature-positive or feature-negative discriminations (in eyelid conditioning) in which delivery of a shock US signaled whether or not a subsequent vibrotactile stimulus would be followed by another, identical shock US. Although the primary purpose of their experiment was to compare the effects of "surprising" and "expected" US presentation, they also tested the effects on responding to the vibrotactile stimulus of presenting (as conditional cues) stimuli previously paired or not paired with the US. As in the present experiment, a stimulus previously paired with the shock conditional cue substituted for that shock as an effective conditional cue.

As Terry and Wagner (1975) noted, however, the ability of a CS to substitute for a US's conditional cue function does not require mediation by an internal representation of that US. That substitution might instead be mediated by overt responding. In the present experiment, for instance, approach to the liquid cup evoked by sucrose delivery (or feedback from that behavior) may have been the true conditional cue in discrimination training. Similar conditioned cup-approach responses evoked by the houselight (e.g., Holland, 1977) may then have mediated discrimination performance in testing.

EXPERIMENT 2

Experiment 2 examined the ability of a CS to substitute for its reinforcer as a conditional cue under circumstances in which it is unlikely that such substitution would be mediated by overt responding common to the CS and the conditional cue itself. First, all rats received two visual stimuli separately paired with the delivery of two solutions differing only in flavor. Subjects then received conditional discrimination training in which delivery of one flavor indicated that a subsequent tone would be reinforced with food pellets but delivery of the other flavor indicated that the subsequent tone would not be reinforced. Thus, the obvious, overt features of responding to the flavor conditional cues were very similar, but the stimulus or perceptual properties of those cues were quite different. Additionally, since all tones were signaled by a flavor, there was little chance of the activity measure's being distorted by the occurrence of different behavior patterns to signaled and unsignaled tones, as may have occurred in Ex-

periment 1. Next, the ability of the two visual CSs to substitute for their associated flavors in controlling discriminative responding to subsequent tones was assessed.

A final test evaluated the ability of "surprising" and "expected" flavor stimuli to serve their conditional cue function in modulating performance to subsequent tones. Terry and Wagner (1975) suggested that a "surprising" conditional cue might be better processed in a short-term working memory system and hence be better remembered when the releaser stimulus was presented. In Experiment 2, we made the delivery of a flavored liquid surprising by preceding it with the visual CS previously paired with the other flavored liquid. Thus, responding to tones preceded by a flavor that, in turn, was preceded by a CS previously paired with a different flavor was compared with responding to tones preceded by a flavor signaled by a CS previously paired with the same flavor.

Method

Subjects and Apparatus. The subjects were 24 experimentally naive Sprague-Dawley rats (12 of each sex), 110-140 days old at the beginning of the experiment. They were maintained at 80% of their free-feeding body weights by limiting their access to food.

The apparatus consisted of six of the chambers used in Experiment 1. The neon glow tubes in the recessed food magazines were illuminated in all phases of Experiment 2. In addition, photocell circuits recorded the time each rat spent with its head at least 6 mm into the magazine during test trials.

Procedure. All rats were first trained to drink from the protruding liquid cup. On the first day of cup training, the cups were filled (15 ml) with 8% sucrose solution before the rats were placed in the chambers; in addition, 10 1-ml presentations of sucrose were given on a VT 1-min schedule. On the second day of cup training, all rats also received 10 1-ml sucrose presentations on a VT 1-min schedule, but the cups were empty when the rats were placed in the chambers.

Next, all rats were given training designed to endow two visual stimuli with the ability to selectively evoke representations of two different flavored reinforcers. In each of 10 80-min sessions, all rats received four 10-sec presentations of the flashing (3/sec) houselight and four 10-sec presentations of the steady signal light, randomly intermixed. For half of the rats (six male and six female), the houselight was reinforced with delivery of 1 ml of a peppermint-flavored sucrose solution, and the signal light was reinforced with 1-ml presentations of a wintergreen-flavored sucrose solution. The other half of the rats received houselight-wintergreen and signal-light/peppermint pairings. The flavored solutions were made by dissolving 50 g of flavored sucrose pellet "flour" (P. J. Noyes Co.) in 1 liter of water. Evidence from previous experiments (Holland, 1981; Forbes & Holland, Note 1), as well as the results of a preference test administered at the conclusion of Experiment 2, indicates that these two solutions are equally preferred.

All rats were then trained to eat food pellets (45 mg, P. J. Noyes Co.) from the recessed food magazine. In a single 20-min session conducted 1-4 h after the final session of the previous phase, the rats received eight 2-pellet presentations on a VT 2.5-min schedule.

Conditional discrimination training was carried out over the next 14 80-min sessions. Four reinforced and four nonreinforced trials were given in each conditional discrimination session. Reinforced trials consisted of a .5-ml delivery of one flavored solution (F+) followed, after a 20-sec trace interval, by a 10-sec 1,500-Hz

tone, which itself was followed immediately by the delivery of two food pellets. Nonreinforced trials consisted of a .5-ml delivery of the other flavored solution (F-) followed, after a 20-sec trace interval, by a nonreinforced 10-sec 1,500-Hz tone. Selection of the flavor presented on reinforced trials was fully counter-balanced, that is, peppermint signaled reinforced tones for half of the rats that had previously received houselight-peppermint pairings and half of the rats that received signal-light/peppermint pairings, and wintergreen signaled reinforced tones for the remaining rats. In addition, the sex of subjects was balanced within each of these subgroups.

All rats then received a single 80-min test session in which the ability of the houselight and signal light to serve as conditional cues in place of their referents was assessed. In this session, the rats received four trials consisting of the 10-sec houselight followed by a 20-sec trace interval and then the 10-sec 1,500-Hz tone, and four trials consisting of the 10-sec signal light followed by a 20-sec trace interval and then the 1,500-Hz tone, randomly intermixed. No liquid or pellets were delivered in this session.

Finally, all rats received two 80-min test sessions in which the ability of surprising or expected flavor presentations to serve as conditional cues for responding to the tone was assessed. Each trial consisted of either a surprising or expected .5-ml flavor cue followed by a 20-sec trace and then the 10-sec 1,500-Hz tone. Flavors were made expected by preceding them with the 10-sec visual stimulus with which they had been paired originally. Flavors were made surprising by preceding them with the 10-sec visual stimulus with which they had not been paired originally. Thus, there were four kinds of test trials, two in which the flavor conditional cue was expected and two in which it was surprising. Each session contained two of each kind of trial, randomly intermixed. No food pellets were delivered in this test phase.

Results

As in Experiment 1, conditioning to the visual CSs in the first conditioning phase was not visible in activity scores. Median activity counts per min during the houselight, signal light, and pre-CS periods over the last two sessions of that phase were 15.8, 18.0, and 21.0, respectively.

Figure 2 shows responding to the reinforced and nonreinforced tone stimuli during conditional discrimination training. By the last two-session block, all rats showed more activity during reinforced tones

Figure 2. Responding during the reinforced (T+) and nonreinforced (T-) tones in the discrimination phase of Experiment 2.

than during nonreinforced tones [$T(24)=0$]. The choice of flavor used to signal reinforcement did not affect the acquisition of the discrimination. Thus, the flavor (or some correlated property) of the liquid deliveries acquired the ability to serve as a conditional cue signaling the occurrence of food after subsequent tone presentation.

As in Experiment 1, the evidence of successful conditional discrimination performance was confined to responding during the tone: over the final two discrimination sessions, median activity responding in the 20-sec interval between liquid presentation and tone presentation was 16.7 counts per min on reinforced trials and 19.9 counts per min on nonreinforced trials. There were no reliable differences in pretone activity rates between reinforced and nonreinforced trials during any two-session block ($T_s \geq 102$). Since there were no reliable differences in pretone activity rates, analyses of during-tone/pretone activity as in Experiment 1 were deemed unnecessary.

The primary data of Experiment 2 were the results of Test 1, in which the ability of the visual CSs to substitute for the flavored liquids as conditional cues was examined. Median activity responding to the tone stimulus was 69.0 counts per min when the tone was preceded by the visual stimulus (CS+) previously paired with the flavor (F+) presented on reinforced trials in the conditional discrimination phase. Median activity was 56.2 counts per min when the tone was preceded by the visual stimulus (CS-) that signaled the flavor (F-) presented on nonreinforced trials in the conditional discrimination phase. This difference was reliable [$T(24)=34$] and was unaffected by whether CS+ was the houselight or signal light, whether F+ was peppermint or wintergreen, or whether the rats were male or female.

The activity data from Test 1 were supported by the measure of time rats spent with their heads in the food magazines. The rats spent 12% of their time in the magazine during the tone after CS+, but only 5% of their time during the tone after CS-. This difference, although small, was reliable [$T(24)=57.5$].

Following Test 1, the rats were given a second test in which the relative effectiveness of surprising and expected conditional cues was examined. Responding to the tone after a surprising F+ (median = 40.5 counts per min) was more frequent than responding to the tone after an expected F+ (30.7 counts/min) [$T(23)=67.5$] (one rat displayed equal responding). Responding to the tone after either a surprising or expected F+ was greater than that after either a surprising (16.5 counts/min) or expected (13.5 counts/min) F- [$T_s(21 \text{ or } 22) < 29$]. Responding was not reliably affected by the surprise value of F- [$T(23)=116$]. Magazine entry responding showed similar trends: the photocells were activated a median of 9% of the time during the tone on surprising F+ trials, 6% of the time on expected F+ trials, and 2% of the

time on both surprising and expected F- trials. However, only the differences between F+ and F- trial responding were reliable [$T_s(21 \text{ or } 22) \leq 61.5$] with this measure.

Discussion

Rats readily learned a conditional discrimination in which the flavor of a solution served as the conditional cue indicating whether or not a subsequent tone presentation would be reinforced with food. Furthermore, visual CSs previously established as signals for those flavors were able to substitute for those flavors themselves in controlling discriminative performance. Since the solutions used as the conditional cues differed only in flavor, it seems plausible that this substitution was mediated by reasonably detailed internal representations evoked by the visual stimuli, rather than by the mere presence or absence of overt responding, as may have been the case in Experiment 1 or in Terry and Wagner's (1975) experiment.

A subsidiary finding of Experiment 2 was that in Test 2 the flavor cue signaling the occurrence of food after the subsequent tone better controlled discriminative responding when that flavor was made surprising (by prior presentation of the visual signal, CS-, for the other flavor) than when it was made expected (by prior presentation of the visual signal, CS+, for that flavor itself). This outcome is consistent with both Terry and Wagner's (1975) data and with their suggestion that events already represented in short-term memory (by virtue of CS+ presentation) might be less well processed and hence less available in memory at the time of tone presentation than surprising events. The results of Experiment 2 are less consistent with an alternative explanation for Terry and Wagner's data offered by Colwill and Dickinson (1980). They claimed that the apparent superiority of surprising events in supporting conditional discrimination performance is the result of stimulus generalization decrement between the conditions of training and those of testing rather than differences in processing of surprising and expected events. In Terry and Wagner's experiment, the conditional cue was presented alone in training. In testing, preceding that cue with a CS+ evoking a potent response might change the stimulus context at the time of conditional cue delivery more than would presenting a CS- that evokes no obvious response. In Experiment 2, however, the visual CSs used to render a flavor surprising had, themselves, been paired with another, equally potent flavor. Thus, within Colwill and Dickinson's account, preceding a flavor cue with either visual stimulus should equally alter the stimulus situation at the time of flavor delivery, and no CS-specific "surprise" effect should be visible, unless it was assumed that a flavor preceded by a signal for it is more like the flavor alone than is that

flavor preceded by a signal for another flavor. That latter assumption, however, shares much with Wagner's (1978) notion. A comparison of the effects of a "surprising" flavor with those of a flavor alone (not conducted here) might more satisfactorily resolve this issue.

Finally, we should point out that the effects of surprising and expected sucrose presentation on discriminative performance were undoubtedly reduced by the opposing effects of presentation of the visual CSs alone. Note, for instance, that in order to make surprising the flavor cue (F-) signaling nonreinforcement of the upcoming tone, that flavor was preceded by a visual signal for the flavor cue (F+) normally signaling reinforcement. Since Test 1 indicated that such a visual signal itself would generate responding to a subsequent tone, it is not unexpected that a surprising F- was no more efficient at suppressing responding to the subsequent tone than an expected F- (which was preceded by a visual CS that was itself capable of suppressing responding to the tone).

GENERAL DISCUSSION

In two experiments, visual stimuli previously paired with flavored solutions substituted for those solutions themselves in controlling performance in simple conditional discriminations. One way of describing this outcome is that pairing of the visual stimuli and flavored solutions endowed the former stimuli with the ability to evoke representations containing some of the same features as the solutions themselves, notably those subsequently acquiring control of discriminative responding. The stimulus specificity of this outcome further indicates that these representations can contain fairly detailed information.

The logic of these experiments resembles that of sensory preconditioning experiments. In such experiments, two, usually neutral, stimuli are first paired in the absence of reinforcement. Conditioned responding is then established to one of those stimuli by pairing it with a third, more potent unconditioned stimulus. Finally, the ability of the other stimulus to also control the responding just established is examined. The observation of responding to that stimulus is frequently interpreted as indicating that otherwise undetected associations were formed between neutral stimuli in the first phase. In the present experiments, associations between neutral stimuli were not at issue, and the transfer of a conditional cue function rather than the simple evocation of a CR was involved. But in both these and sensory preconditioning experiments, the ability of pairings of two stimuli to endow one with the ability to later substitute for the other is of interest.

The conditional cue function established to the solutions in these experiments deserves further comment. It might be claimed that discriminative re-

sponding to the tones reflected merely the acquisition of excitation or inhibition to the flavored solutions, which then summed with subthreshold tone-evoked responding. But, several factors argue against that interpretation. First, activity responding during or after the solutions did not differ depending on whether the solution predicted the eventual occurrence or nonoccurrence of food. Although it might be further argued that the solutions controlled responding that was not detected by our activity transducers (as with visual CSs), it is worth noting that previous evidence (Holland, 1977; Ross & Holland, 1981) indicates that summation of conditioning to CSs controlling different response tendencies results in competition among those responses and, hence, suppression of any particular measured response. Thus, the summation of excitation to a food-predicting solution and to the tone would probably not yield greater activity responding than that controlled by the tone alone. Second, other experiments (e.g., Looney & Griffin, 1978; Ross & Holland, 1981) indicate that, in serial conditioned discriminations of this type, a conditional cue's ability to control discriminative responding to a subsequent stimulus is not positively correlated with its own ability to evoke conditioned behavior. Instead, these cues seem to acquire a conditional, rule-type function (cf. Carter & Werner, 1978) often described as "setting the occasion" for responding to subsequent stimuli (e.g., Moore, Newman, & Glasgow, 1969; Ross & Holland, 1981).

Regardless of the precise nature of the solutions' control over responding to the tone, the ability of visual CSs previously paired with those solutions to substitute for them in controlling discriminative performance complements the findings of Forbes and Holland (Note 1) and Holland (1981) in suggesting that evoked or "retrieval-primed" representations of stimuli can substitute for those stimuli themselves in a variety of conditioning functions. Furthermore, the results of Experiment 2 support Wagner's (1978) claim that the activity of event representations in memory is affected by their surprise value. These kinds of data—taken together with data indicating that postconditioning revaluation of unconditioned stimuli often alters behavior evoked by CSs (see Rescorla & Holland, 1982) and data suggesting that discriminative control is enhanced if explicit discriminative stimuli also evoke distinct representations of specific outcomes (e.g., Peterson, Wheeler, & Trapold, 1980)—further define the roles of event representation in conditioning and encourage the use of such a construct in theories of conditioning.

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