Unpredicted food produces a mode of behavior that affects rats' subsequent reactions to a conditioned stimulus: A behavior-system approach to "context blocking"

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The present experiments explored the relation between a mode of behavior produced by unpredicted presentations of an unconditioned stimulus (US) and subsequent interference with responding to a conditioned stimulus (CS) (the context-blocking effect). The US was food, the CS was a moving ball bearing, and the subjects were rats. The typical response to a moving bearing that predicts food is predatory interaction, and the behaviors that developed under unpredicted US presentations involved focused search and waiting oriented to the food tray. Experiment 1 manipulated the number of unpredicted food presentations and showed that the reduction in subsequent bearing contacts was more clearly related to the occurrence of initial food-tray behavior than to the number of prior food presentations. Experiments 2 and 3 manipulated the conditioning of food-tray behavior while holding constant the number of prior food presentations, and again showed a strong inverse relationship between initial food-tray behavior and ball-bearing contact. The latter experiments also indicated that the locus of interference with bearing-directed behavior was neither primarily central (associative or attentional) nor peripheral (motor interference), but resulted from the incompatibility of two modes of food-getting behavior, a more general predatory search mode versus a mode of focal search and waiting. A behavior-system account of these results does not preclude an associative basis for context-blocking effects, but it argues that such effects may occur at several levels and must function within appetitive structures underlying the animal's food-getting behavior.

Unpredicted presentations of food (the unconditioned stimulus; US) prior to training with a predictive stimulus (the conditioned stimulus; CS) can retard the emergence and reduce the expression of autoshaped behavior directed to the predictive stimulus (e.g., Balsam, 1985; Balsam & Schwartz, 1981; Downing & Neuringer, 1976; Engberg, Hansen, Welker, & Thomas, 1972; Tomie, 1976, 1981). A popular explanation for this effect is based on an assumption that the total associative strength supported by a particular US is limited (Rescorla & Wagner, 1972; see also Mackintosh, 1975). In the context-blocking view, unpredicted presentations of the US produce an association between the US and the context (the stimulus surround in the experimental situation), thereby decreasing the available associative strength and blocking subsequent conditioning of associations between the US and a subsequent discrete CS (Kamin, 1969; Tomie, 1981).

Data supporting the context-blocking account show that the decremental effect of prior US deliveries is a direct function of their number (e.g., Balsam & Schwartz,

1981), and that changing the stimulus context prior to presenting a CS (thereby presumably removing the conditioned contextual stimuli) increases conditioning to the CS (Tomie, 1976, 1981). However, several manipulations that affect more traditional examples of blocking using discrete CSs produce different results in context-blocking experiments, thereby questioning whether these phenomena can be explained by a common theory (e.g., Randich & LoLordo, 1979; Tomie, 1981).

Most frequently, context blocking has been treated as an abstract general process, with little attention to either the precise controlling stimuli or the behaviors involved. There has been only slight consideration that US-alone presentations may interfere with subsequent conditioning at levels other than central association (e.g., Gibbon & Balsam, 1981). Yet, from an evolutionary view, it seems unlikely that a general mechanism exists the operation of which *necessitates* that unpredicted food interfere with the subsequent control of behavior by a predictive stimulus that is both more salient and a better predictor of food than the general context.

Consider two imaginary scenarios involving a nectar-feeding bird that discovers a new food source in a small white flower randomly distributed among other white flowers in a particular field. In the first scenario, once the bird reaches the field, it approaches all white flowers

This research was supported in part by NSF Grants 82 10139 and 84 11445. I thank Lexie Peterson, Donna Washburne, and Frank Adams for assistance, and Graham Davey, Jim Dougan, Heather Eisthen, Blaine Peden, Ben Williams, and Gary Lucas for comments. Reprints can be obtained from William Timberlake, Department of Psychology, Indiana University, Bloomington, IN 47405.

as it comes to them. The initial controlling association is only between the presence of food and the general context of the field. If the target flowers suddenly changed color, we would not be surprised to find the birds beginning to use this new signal immediately. Furthermore, we might expect the opposite of a context-blocking effect; experienced birds might well be more efficient at exploiting this new cue than inexperienced birds.

In the second scenario, suppose the target white flowers were reliably located near a tall plant with purple blossoms. Because of the predictable physical proximity of the white flowers and the tall plants, we would expect a specific association between them, and a search strategy based on approach to the tall plants. In this case, if the white flowers suddenly turned color, we might expect a context-blocking-like phenomenon. The birds probably would not switch to this new signal immediately, and we might expect that the more experienced birds would be less efficient in responding to this new color when it was presented alone.

Though these are only stories, they suggest that the effects of US-alone presentations on subsequent conditioning should vary with the nature of the system of behavior under study (including the stimulus sensitivities and the organization and sequences of behavior typical of that system), and with the way in which the expression of that system is supported and altered by environmental stimuli and contingencies (e.g., Timberlake, 1983a, 1984). To take a concrete example, we have been studying the feeding system in rats, in particular the ability of a moving stimulus (a rolling ball bearing) predicting food to elicit components of predatory and handling reactions (Timberlake, 1983b; Timberlake & Melcer, 1986; Timberlake, Wahl, & King, 1982). Our data show that the expression of the feeding system is structured so that a moving bearing that reliably precedes food by more than 4 sec is highly likely to elicit predatory behavior directed to itself; however, as the interval between onset of the moving stimulus and food decreases, the rats become more likely to attend to and/or intensify behavior related to the food tray rather than interact with the moving stimulus.

Our interpretation of this evidence is based on the assumption that predatory and food-tray behaviors represent different behavioral modes (motivational substates). Food-tray behavior is related to focal search and waiting, a mode elicited by a high probability of food in a particular location. Predatory behavior is related to a more general and costly search mode elicited by the potential appearance of an appropriate predatory object. Longer intervals between the appearance of the predictive bearing and food elicit predation-related search. Shorter intervals to food override this reaction in favor of behaviors related to obtaining food in the food tray (focal search and waiting). The predatory and focal search modes are distinct, coherent, and ordered in the experimental circumstances. If the rat goes to the bearing first, it eventually goes to the food tray (even if food has not yet been delivered).

However, once the rat goes to the food tray, it rarely leaves the tray prior to eating.

It should be emphasized that the CS-US interval for switching from one mode of behavior to another is not a fixed characteristic of the feeding system, but is determined by the interaction of system characteristics with the eliciting stimulus conditions. In the absence of a prey stimulus, the general search behavior consists only of checking large portions of the environment, and the interval over which focal food-tray search occurs is much longer. Thus, "goal tracking" behavior has been reported at longer intervals (e.g., Boakes, 1977; Farwell & Ayres, 1979; Reberg, Mann, & Innis, 1977). On the other hand, given a live prey item, a focal search mode may be expressed only in digging the prey out of hiding or in area-restricted search following a kill.

The present research explored the way in which the sequence of general predatory and focal search modes interacted with a typical context-blocking paradigm in which US-alone presentations preceded conditioning with a predictive ball bearing. My basic assumption was that US-alone presentations would condition food-tray behavior related to focal search and waiting, and that some aspect of this process would interfere with subsequent behavior directed to the bearing. Thus, the behavior-system view predicts that interference with responding to the CS should be closely related to the levels of food-tray behavior conditioned during US-alone presentations.

My second assumption was that interference with bearing interaction would result from the incompatibility of the modes of general predatory search and focal (food-tray) search, rather than from a central failure of attention or association, or a strict motor interference of behaviors. Two predictions follow reasonably from this assumption. First, though US-alone training should interfere with interaction with the bearing, the bearing is still likely to develop some control of focal search and waiting behaviors because it is a better predictor of food delivery than the simple passage of time. This implies that there should be initiation or intensification of food-tray behavior when the bearing is presented.

Second, in extinction, as the probability of food goes to zero, behaviors related to focal search and waiting should be replaced by a more general search mode. Because the bearing has been associated with the food system by previous pairings and strongly instigates predatory behavior, we would expect the majority of the increase in active search to consist of bearing-directed behavior. In other words, the animal will move "back up" the sequence of behaviors leading from search to ingestion. Initially, it will go from focal search and wait to more general predatory search, and from there to escape behaviors and/or quiescence as extinction continues. If there were no bearing, and thus less instigation for predatory behavior, we might anticipate that the animal would maintain some form of food-tray-directed behavior for a longer time. In this case, the only form of the competing general

search mode would be a more general exploration of the chamber.

These predictions can be contrasted with several other possible outcomes. If US-alone presentations produce central interference with subsequent stimuli as candidates for association, then there should be no noticeable effect of the bearing on food-tray behavior, and extinction should consist simply of its slow decline. On the other hand, if the interference is based at the level of incompatible responses, then conditioning may occur to the bearing (and may well be slightly observable). However, it should be either not expressed in extinction, because the eliciting qualities of the ball bearing are extinguished, or it should alternate with food-tray behavior as first one and then the other decreases in strength with unrewarded expression.

The specific aims of the present experiments were to explore the importance of focal search-and-wait behaviors in mediating the effects of US-alone presentations, and to determine whether interference occurred at central, peripheral, or modal (predatory vs. focal search) levels. Experiment 1 presented different groups with different numbers of unpredicted food deliveries and determined their effect on food-tray behavior and subsequent responding to the CS of a moving bearing. Experiments 2 and 3 held constant the number of US-alone presentations and manipulated the conditioning of focal search behaviors to separate more clearly the causation of the decremental effects of unpredicted US presentations. In addition, in both Experiment 2 and Experiment 3, an extinction condition was run to determine the level at which US-alone presentations interfered with bearing-directed behavior.

EXPERIMENT 1

The purpose of the first experiment was to establish whether interference with subsequent conditioning by prior unpredicted food (US) deliveries (1) could be obtained using a moving ball bearing as the CS predicting food; (2) was directly related to the number of unpredicted food deliveries, (3) was directly related to the conditioning of food-tray behavior (focal search and waiting); and (4) reflected the absence of any conditioning to the bearing, or merely the absence of expression of such conditioning in CS-directed behavior.

Different groups of rats received 1, 14, or 50 presentations of food pellets (Groups Low, Medium, and High US exposure) prior to pairings of a ball bearing (CS) with pellet delivery. Both the general context-blocking view and the behavior-system approach predicted that the level of expressed conditioning to a subsequent CS generally should be inversely related to the number of US-alone presentations. Context blocking predicts this outcome because a greater number of US-alone presentations should use up more of the available associative strength. The behavior-system approach argues that the conditioning of behaviors related to focal search should, other things being equal, be a function of the number of US presentations. However, the behavior-system view also holds that

interference with subsequent conditioning should be more accurately predicted by the actual levels of food-tray behavior produced by US-alone presentations; these behaviors reflect the actual competing strength of the focal search-and-waiting mode in this situation.

Method

Subjects. The subjects were 15 naive female Sprague-Dawley albino rats, housed one per cage under a 12:12 h light:dark cycle. One rat in Group Low became ill shortly after the experiment began and was eliminated. The rats were adapted to a 23-h food-deprivation regimen over a period of 3 weeks. On this deprivation schedule, they received sufficient laboratory chow in their home cages following the experimental session to maintain their body-weights at 85% of ad-lib weight.

Apparatus. The apparatus has been described elsewhere (Timberlake, 1983b). It was a rectangular sheet-metal box, 61×30×30 cm, with a Plexiglas top and front. Ball bearings entered the apparatus in a V-shaped channel that ran the length of the chamber and was slanted 6° from entry to exit. The floor of the apparatus was also slanted toward the channel so that a bearing dropped anywhere in the chamber would reenter the channel and roll out. The channel was located 9 cm from and parallel to the front wall. Once dispensed, a bearing took approximately 2 sec to enter the chamber and 3.1 sec to roll through it, if undisturbed. Food was available in a 2.0×5.0×1.8 cm deep receptacle (food tray) centered in the wall with the exit hole. The observer sat 1 m from the front wall of the apparatus. Data-logging and control equipment were located in the room with the apparatus.

Procedure. The experimental procedure consisted of four phases: pretraining, baseline, feeder training, and pairing. Pretraining consisted of a single day of placement of the animals in the chamber for 8 min with no food or ball bearing present. During baseline, the animals received four sessions of 10 ball bearings a day presented on a variable-time (VT) 45-sec schedule. On the basis of their median number of contacts on the last 3 days of baseline, the rats were divided into three matched groups of 5 rats. Group Low subsequently was reduced to 4 rats by illness.

During feeder training, Group Low received no food on Day 1 and 1 45-mg Noyes pellet on Day 2; the animals remained in the apparatus for 8 min on each day. Group Medium received 1 pellet on Day 1, but 13 pellets on Day 2, the first on entry to the chamber, the next 6 while within 3 cm of and oriented toward the food tray, the next 3 while the head and body were turned away from the tray, and the final 3 when the animal was more than 12 cm from the food tray; all food deliveries were on an approximate VT 20-sec schedule (audible clicks were produced by a tape timer, but food delivery was by hand and was subject to the additional criteria noted above). Group High received 25 pellets on each day for a total of 50. On each day, each rat in this group received successively 1 pellet at the beginning of the session, 6 while within 3 cm of and oriented toward the food tray, 6 while the head and body were turned away from the tray, and 12 while the animal was more than 12 cm from the tray.

During the subsequent pairing condition, all the groups received 14 days of 10 pairings a day between the presentations of the ball bearings and food on a modified VT 45-sec schedule. The pairings consisted of delivering the food pellet when the ball bearing exited the chamber. The VT tape was stopped while the bearing was in the chamber. A 2-min limit was imposed on the rat's interaction with the bearing on each trial, at which point the experimenter opened the top of the apparatus, and used the end of a wooden ruler to gently push the bearing from the animal's paws. This entire sequence was rarely necessary. On the infrequent occasions on which the animal held the bearing beyond the time limit, opening the top of the chamber or inserting the ruler usually stopped the interaction.

Data were obtained by direct observation of the animals' behavior by one of two paid observers. The observers were trained by the author and did not know the hypotheses of the study. The coding agreement with the author during tests was .94 or better (computed on agreement of presence and absence of category instances each trial). On each trial, the observer coded the animal's behavior into categories related to bearing contact (touch the bearing with the nose, paws, or mouth, carry, and chew), food-tray behavior (remain or approach to within 3 cm of the food tray, nose in food tray, lie with front paws and head in food tray), and other categories (including orient toward and approach the bearing, and sniff and dig in the entrance and exit holes). A more extensive definition of most categories can be found in Timberlake et al. (1982).

Results and Discussion

Figure 1 shows the change in the average number of trials on which Groups Low, Medium, and High (US exposure) contacted the bearing during each pairing session. The change scores were computed by subtracting the median of the last three baseline trials for each animal from its scores during each pairing session. Although the groups did not differ significantly in baseline, change scores were used because the acquisition effects were easier to compare visually. Figure 1 indicates that, relative to Group Medium, both a very small number of food presentations (Group Low) and a larger number of food presentations (Group High) retarded the development of subsequent bearing-directed behavior. However, only Group High appeared to be permanently affected. Both Group Low and Group Medium significantly increased bearing contact over baseline levels (comparing medians of the last three trials in baseline and pairing conditions) [$t(4) = 5.43, p < .01$, and $t(3) = 3.82, p < .05$], but Group High did not [$t(4) < 1, p > .10$].

An analysis of variance over the pairing sessions showed a significant overall increase in contacts [$F(13,143) = 7.77, p < .01$], but failed to reveal significant differences among the three groups [$F(2,11) = 1.77, p > .10$]. The absence of a significant groups effect appeared to be due to the high degree of variability in the scores of individual animals. For example, the median trials with a bearing contact over the last three ses-

Figure 1. Average change in number of trials with a ball bearing contact for Groups Low (1 pellet), Medium (14 pellets), and High (52 pellets). Each animal's change score was calculated by subtracting the median baseline score from the score for each pairing session (Experiment 1).

Figure 2. Average change in number of trials with initial food-tray behavior for Groups Low (1 pellet), Medium (14 pellets), and High (52 pellets). Each animal's change score was calculated by subtracting the median baseline score from the results for each pairing session (Experiment 1).

sions were 10, 9, 8, and 1 for subjects in Group Low, 10, 10, 9, 8, and 7 for those in Group Medium, and 10, 10, 7, 2, and 1 for those in Group High. This degree of variability shows that number of unpredicted US presentations was not as strong a controller of behavior as might have been anticipated. In all groups, some animals readily conditioned to the bearing and others did not.

Figure 2 shows the change in average number of trials on which Groups Low, Medium, and High showed initial food-tray behavior when the bearing was presented. Again, the change scores were computed by subtracting the three-trial baseline medians from the scores on each session during pairing. Initial food-tray activity was scored on a given trial if the animal's head was within 3 cm of the food tray prior to any contact with the bearing. Food-tray activity that followed contact with the bearing was not counted in this analysis because it did not serve as an alternative to contact behavior. It can be seen that the order of food-tray scores was the inverse of the contact scores in Figure 1, and the results of the analyses were similar. The initial food-tray behaviors increased significantly over baseline for all groups (all p s $< .05$), but did not differ significantly between groups [$F(2,11) = 1.54, p > .10$]. There was also a significant decrease in food-tray trials across sessions [$F(13,143) = 2.74, p < .05$].

These data provided marginal support for the prediction that the decremental effects of US-alone presentations should be directly related to their number. Part of the reason for the weakness of this relation was the relative retardation of conditioning in Group Low. Apparently a single US presentation is not sufficient to allow conditioning to proceed rapidly. It might be speculated that the feeding system was not adequately engaged at a general motivational level or in terms of specific attention to the food tray by the discovery of a single pellet in an unfamiliar environment. The remainder of the lack of a significant relation was due to high variability in the scores of individual animals.

On the other hand, these data are compatible with the notion that the prior emergence of food-tray behavior in-

terfered with the development of bearing-directed behavior. The high level of food-tray behavior during the initial sessions shown in Figure 2 indicates that food-tray activity developed under US-alone presentations. Furthermore, the changes in the form and intensity of behavior that often occurred when the bearing was presented indicated that the bearing gained some control of food-tray activity. Most importantly, there was a marked inverse relation between food-tray activity and bearing contact both among groups (see Figures 1 and 2) and across individual subjects [$r(14) = -.88, p < .01$]. However, the correlational nature of these data makes any causal inference highly speculative.

EXPERIMENT 2

Experiment 1 showed that prior unpredicted food presentations interfered with conditioned contact of a moving ball bearing that subsequently predicted food. However, individual scores suggested that the decremental effects of unpredicted food presentations were more closely related to the animals' food-tray behavior than to the number of prior food presentations. Animals that showed a retardation effect were those that exhibited initial food-tray behavior on each trial, whereas animals with less initial commitment to the food tray more often showed typical development of contact to the bearing.

The correlational nature of these data prevents the firm conclusion that focal search-and-wait behaviors oriented to the food tray were related to the cause of the decremental effects of unpredicted US presentations. Such a conclusion requires the independent manipulation of the conditioning of food-tray behavior and the number of prior food presentations. Experiment 2 dissociated number of US presentations and conditioned food-tray behavior by presenting food to experienced animals under different opportunities for conditioning food-tray behavior. The animals from Experiment 1 were divided randomly into two equal groups, each of which received 80 additional pellet presentations. Group Close received its pellets on a VT 20-sec schedule provided the animal was within 3 cm of the food tray. Group Away received its pellets on the same basic schedule subject to the additional requirement that the animal be at least 12 cm from the food-tray.

A general context-blocking view predicts that both groups should behave the same, since both received the same number of unpredicted US presentations. Furthermore, the interpolated food presentations should have no effect on responding because all the associative strength of the US should have been used up by the conditioning reported in Experiment 1. In contrast, the behavior-system approach predicts that because Group Close should show a greater increase in food-tray behavior, it should subsequently show less bearing contact than Group Away.

By extinguishing the animals in the presence of the bearing, Experiment 2 also examined the level at which US-alone presentations interfered with behavior directed

toward the bearing. If the level of interference is largely central (associative), then extinction should consist of a slow decrease in food-tray behavior. If the level of interference is peripheral, then extinction should consist of either a slow decrease in food-tray behavior or an oscillation of food-tray and bearing-directed behavior as first one and then the other decreased in strength. Finally, if interference results from the incompatibility of focal and predatory search, then eliminating food should rapidly throw the animals in Group Close back into a more general search mode; this should produce a rapid decrease in food-tray behavior and a rapid rise in bearing-directed behavior followed by a slower decline as the absence of food became more certain.

Method

Subjects and Apparatus. The subjects, housing conditions, and apparatus were the same as in Experiment 1.

Procedure. The 14 rats that completed Experiment 1 were randomly assigned to two equal groups, with the requirement that each of the three prior groups be approximately equally represented in the new groups. Both groups then received 4 additional days of feeder training, followed by 4 additional days of pairings between the ball bearing and food and 10 extinction trials with ball bearings alone. During feeder training, both groups received 20 pellets a day delivered on an approximate VT 20-sec schedule. Once food had "set up," animals in Group Close had to be within 3 cm of the food tray and animals in Group Away had to be more than 12 cm from the food tray before food was delivered and the interfood interval began again. Because of the additional requirement, on the 1st day of feeder training, the median interfood interval was close to 60 sec for Group Away. However, by the 3rd day, the median interfood interval was 20 sec for both groups. Other procedural details were the same as in Experiment 1.

Results and Discussion

Figure 3 shows the change in frequency of trials with a ball-bearing contact over the four re-pairing sessions and 10 extinction sessions following the additional feeder training. During re-pairing, both groups had fewer contact trials than before the additional feeder training [$F(1,12) = 10.41, p < .01$] and both groups gradually

Figure 3. Average change in the number of trials with a contact for Groups Close and Away during re-pairing and extinction (Experiment 2). Change was evaluated by subtracting re-pairing scores from the median scores on Trials 12-14 of Experiment 1.

increased their contact trials over sessions [$F(3,36) = 6.21, p < .01$]. However, as predicted by a mode competition view, Group Close had significantly fewer contact trials than Group Away [$F(1,12) = 4.90, p < .05$]. Group Away recovered previous levels of bearing contact after 1 day of the re-pairing condition. In contrast, Group Close did not recover previous contact levels over the 4 days of re-pairing.

During extinction, both groups decreased their overall contacts, but did not differ from each other [$F(1,9) < 1, p > .10$]. Inspection of the initial extinction trials shows that Group Close increased contact with the bearing whereas Group Away did not. A comparison of the median of the last three pairing trials and the first three extinction trials confirmed a significant increase in bearing contacts for Group Close but not for Group Away [$ts(6) = 2.19$ and $< 1, ps < .05$ and $> .10$, one-tailed test].

Figure 4 shows the change in frequency of trials with initial food-tray behavior. The results mirrored those for ball-bearing contact. During re-pairing, both groups had more trials with initial food-tray behavior than they had had before the additional feeder training [$F(1,12) = 17.34, p < .01$], and both groups decreased the number of trials with initial food-tray behavior over days [$F(3,36) = 4.35, p < .05$]. Group Close had more trials with initial food-tray behavior than did Group Away [$F(1,12) = 7.02, p < .05$]. During extinction, both groups dropped out food-tray trials, which did not differ significantly from zero [$F(1,12) < 1, p > .10$]. However, the decline was faster for Group Away. A comparison of the medians of the last three pairing trials and the first three extinction trials showed a significant decrease in food-tray behavior for Group Close but not for Group Away [$ts(6) = 3.41$ and $1.19, ps < .01$ and $> .10$].

The effect of interpolated food presentations supported the importance of focal search and wait as a mediator of the interfering effects of US-alone trials. Animals allowed to develop food-tray behaviors during pellet presentations (Group Close) showed less bearing-directed behavior than animals not rewarded for food-tray behavior. In extinc-

tion, the immediate increase in bearing behavior and decrease in food-tray behavior in Group Close, and the subsequent lack of differentiation between the two groups, argued against either a central or peripheral account of interference. Interference appeared to be due to the development of a particular mode of behavior (focal search and wait). When food was discontinued, the animals rapidly switched to the better supported predatory search mode. However, these conclusions should be evaluated cautiously because of the prior conditioning the present subjects received in Experiment 1.

EXPERIMENT 3

Experiment 2 indicated that the development of food-tray behavior was a crucial element in the retardation and reduction effects of unpredicted US presentations in the present paradigm. However, the experiment used only experienced animals. The purpose of Experiment 3 was to further test the importance of food-tray behavior by delivering the US-alone presentations to naive animals. Two groups of rats received 112 unpredicted food presentations prior to any pairing of the ball bearing and food. Group Close received the food deliveries when they were within 3 cm of the food tray. Group Away received all but 32 of its 112 pellets when at least 12 cm from the food tray.

Method

Subjects and Apparatus. The subjects were 12 female albino rats, 90 days old at the start of the experiment. They were housed the same as those in Experiment 1 and were trained in the same apparatus.

Procedure. The animals were placed on a food-deprivation schedule, as in Experiment 1. The procedure consisted of five phases: pretraining, baseline, feeder training, pairing, and extinction. Pretraining consisted of 2 days of animal placement in the chamber for 8 min with no food or bearing present, followed by 2 further days on which four 45-mg Noyes pellets were placed in the food tray. After pretraining, the animals received four sessions of 10 ball bearings a day presented on a VT 45-sec schedule, followed by 4 days of feeder training. On each day of feeder training 6 pellets were presented in the food tray to begin the session and then 20 pellets were presented on approximately a VT 20-sec schedule. Group Close received pellets only when within 3 cm of the food tray. Group Away received the pellets only when they were more than 12 cm from the food tray. As in Experiment 2, by Day 3, the median interpellet delivery time was 20 sec for both groups. Both groups then received 12 sessions of pairings of the ball bearing and food on a VT 45-sec schedule and 14 sessions of extinction, during which the ball bearing was presented alone. The specific procedures for pairing were the same as in Experiment 1.

Results and Discussion

Figure 5 shows the average contacts for the Close and Away groups during baseline (mean of 3-day medians), acquisition, and extinction. Although there was no significant difference between the baseline scores of the two groups [$F(1,10) < 1, p > .10$], there was a considerable difference in their distributions, so an analysis of covariance was used to compare the groups during acquisition and extinction. In acquisition, Group Away con-

Figure 4. Average change in the number of trials with initial food-tray behavior for Groups Close and Away during re-pairing and extinction (Experiment 2). Change was evaluated by subtracting the re-pairing scores from the median scores on Trials 12-14 of Experiment 1.

tacted the bearing significantly more often than did Group Close [$F(1,9) = 6.76, p < .05$], and there was a significant increase in number of contacts over days [$F(11,110) = 5.05, p < .01$]. Group Close also showed significantly more trials to first bearing contact than did Group Away; the mean trials were 8.5 to 1.8 [$t(10) = 1.80, p < .05$].

In extinction, contact tended to decrease in both groups [$F(9,90) = 1.80, .10 > p > .05$], and the groups did not differ in total contacts [$F(1,9) = .30, p > .10$]. However, a comparison of the medians of the last three pairing trials and the first three extinction trials showed a significant increase in bearing-directed behavior for Group Close but not for Group Away [$ts(5) = 2.74$ and $< 1, ps < .05$ and $> .10$].

Figure 6 shows the average number of trials per session on which each group of animals engaged in food-tray behavior not preceded by bearing contact. Baseline scores were again the mean of three session medians. During pairing, Group Close showed significantly more trials with initial food-tray behavior than did Group Away [$F(1,10) = 4.56, p < .05$], and both groups decreased food-tray behavior over trials [$F(11,110) = 4.63, p < .01$]. In extinction, food-tray behavior dropped out for both groups, with no difference between them [$F(1,10) < 1, p > .10$]. However, a comparison of the medians of the last three pairing trials and the first three extinction trials showed a significant decrease in food-tray behavior for Group Close but not for Group Away [$ts(5) = 3.17$ and $> 1, ps < .05$ and $> .10$].

In sum, the way in which unpredicted food was delivered critically influenced the development of conditioned behavior directed to a subsequent CS. If the animal developed food-tray behavior during presentations of the US, then subsequent expression of bearing-directed behavior was impaired. Although there was no appropriate comparison group in the present study, the more than 100 pellet presentations for Group Away did not decrease the final level of conditioned contact to the bearing relative to prior studies that had not used extensive unpredicted food deliveries (e.g., Timberlake, 1983b; Timberlake

Figure 5. Average number of trials with a ball bearing contact for Groups Close and Away during baseline, pairing, and extinction (Experiment 3).

Figure 6. Average number of trials with initial food-tray behavior for Groups Close and Away during baseline, pairing, and extinction (Experiment 3).

et al., 1982). Furthermore, the rapid increase in bearing contacts and decrease in food-tray behavior in extinction by Group Close and the lack of overall difference in bearing contacts between the Close and Away groups support the argument that the development of bearing-directed behavior was not prevented, but was only reduced in expression, by the conditioning of food-tray behavior.

GENERAL DISCUSSION

These experiments addressed two major objectives. The first was to examine the role of focal search and waiting behaviors in mediating the interference of US-alone presentations with subsequent conditioning to a ball-bearing CS. When unpredicted food deliveries occurred either independently of the rats' behavior (Experiment 1) or contingent on close proximity to the food tray (Group Close in Experiments 2 and 3), most animals developed extensive food-tray activities. Rats dug in the food tray, poked it with their noses, rested on their haunches in front of it, and leaned against the rim with head and paws inside it. An inverse relation between food-tray activities and bearing contact was found both at the level of individual differences (Experiment 1) and at the group level as a function of whether animals received US-alone presentations while close to or away from the food tray (Experiments 2 and 3). Under all circumstances, rats that showed higher levels of initial food-tray behavior showed lower levels of bearing contact.

These results show that US-alone training does not invariably interfere with behavior to a subsequent CS. In the present case, interference appeared to depend on the nature of the behaviors that emerged during the US-alone training. However, prior to reaching a firm conclusion about the causal importance of food-tray behavior, we must consider whether the inverse relation between bearing-directed and food-tray behavior was a procedural artifact. For example, was this inverse relation forced by an either/or coding scheme or the nature of the apparatus? Apparently not, because the coding scheme did not

require any behavior to be coded, and the apparatus allowed animals to continue to groom, rear, walk about, pause, and sniff holes, walls, and bearing track, just as they did during the intertrial interval. Furthermore, there was enough time for the animals to go first to the hopper and then to the bearing, but they did not.

Another possibility is that delivering pellets to Group Away in pretraining only when the animals were close to the food tray produced behavior that made them less likely to see the bearing, and, thus, effectively decreased their number of opportunities to contact it. However, it seemed to me that the animals were aware of the presence of the bearing. All animals were familiar with the sound of the bearing from baseline presentations, and it could be heard clearly as it rolled through the chamber. Most animals that showed initial food-tray behavior actually seemed to avoid looking at the bearing, as though it might attract them away from the food tray (see Boakes, Poli, Lockwood, & Goodall, 1978); instead they used the sound as a signal to dig and nose in the tray.

Finally, it might be argued that the subjects in Group Away were closer to the ball bearing during its presentation, and thus, merely on the basis of proximity to the bearing, this group should have contacted the bearing more. In fact, the animals most likely to be close to the bearing on each trial were in Group Close. If an animal was at the food tray, the bearing inevitably rolled by at a distance of 4 cm or less as it exited the chamber. Group Away, on the other hand, never had to come closer than about 19 cm, and a 10-cm distance was fairly typical until the animal approached the bearing. In short, the inverse relation between food-tray behavior and bearing contact was unforced. Thus, food-tray behavior most likely represented a competing alternative to bearing interaction.

The second objective of these experiments was to determine the level at which US-alone presentations interfered with bearing-directed behavior. For example, did food-tray behavior preclude any conditioning to the moving ball bearing, or was the interference simply a question of how conditioning was expressed in behavior? There are three indications that interference was primarily in terms of expression rather than conditioning. First, some bearing-directed behavior was conditioned in nearly all animals; thus, in no case was association blocked completely. Second, animals engaged in food-tray behavior tended to change and intensify their behavior when the bearing rolled by, something they should not have done to a familiar stimulus if conditioning to the bearing was blocked by prior learning. The form of this behavior change was difficult to establish *a priori* as a single coherent category, so it was not coded systematically; but the experimenters noted many examples, including onset of digging, increased nosing, or insertion of forepaws and head into the food tray. Third, the bearing contact scores in extinction for Group Close showed an immediate rise to the level of Group Away in both Experiments 2 and 3 and an indistinguishable course of subsequent extinction;

both outcomes are unlikely unless similar conditioning had previously occurred to the bearing. Taken together, this evidence supports the notion that conditioning to the bearing occurred, but that the form of expression was determined by other factors.

The remaining question to resolve is whether interference with the expression of bearing-directed behavior occurred at the peripheral motor level (because the animal simply was unable to perform two behaviors at once), or whether the interference occurred at a higher level of response organization. There are several indications that the periphery was not the primary level of interference. First, there was no necessary peripheral interference, because the animals were perfectly capable of both interacting with the ball bearing and engaging in food-tray behavior during the same CS. Many of the animals in Group Away demonstrated this possibility by interacting with the bearing and then the food tray, in that order. The critical determinant of interference was whether the animal began the food-tray behavior first; if so, it almost never engaged the ball bearing on that trial. Thus, interference was related to the order of two sets of possible behaviors, rather than to the physical impossibility of engaging in each.

Second, a peripheral interference model does not explain readily why the animals in Group Close rapidly increased ball-bearing behavior in extinction to the level of Group Away, and then showed roughly the same course of extinction. It might be argued that the first few trials without food reduced the tendency to go to the food tray sufficiently for the tendency to go to the bearing (assuming it wasn't extinguished at the same time) to become momentarily stronger. But this extinction-only-by-expression process should repeat itself, producing a regular oscillation between going to the bearing and going to the food tray. No such oscillation was observed.

Third, the behaviors directed to the food-tray, though not random, were not even approximately identical from trial to trial. On some trials, the animal gnawed on the rim of the food tray; on others, it buried its nose in a corner; and on still others, it dug at the back. Similar differences occurred in interactions with the bearing. This diversity suggests that what is conditioned is not a particular behavior, but a set of behaviors, a mode or strategy of behaving. In this view, the interference that occurred was at the level of a behavioral mode or strategy rather than a particular peripheral behavior. Predictable and frequent food appeared to produce a focal search-and-wait mode with the food-tray as target, whereas less predictable and infrequent food tended to produce more general search behaviors. In the presence of a moving stimulus, these search behaviors were focused at the level of predation.

A Behavior-System Interpretation

On the basis of these and other data (e.g., Timberlake et al., 1982), it appears that both bearing contact and food-tray behavior can occur under conditions in which presen-

tation of a bearing predicts food. If nearly all food deliveries are predicted well in advance by the ball bearing, then bearing contact typically precedes food-tray behavior; but after presentations of food alone (the present data) or the use of a short interstimulus interval (Timberlake et al., 1982), food-tray behavior typically supersedes bearing contact except during extinction.

Obviously these data are not compatible with a typical context-blocking view, which argues only that unpredicted presentations of a US use up its associative strength by the conditioning of the background stimuli (context). In these data, US-alone presentations appeared to alter the expression of subsequent conditioning rather than prevent it. Interference with subsequent conditioning was related to the behaviors produced, not primarily to the number of US-alone presentations. Finally, the context-blocking view says nothing about the form of the behavior produced by US-alone presentations, or why the food-tray area rather than the general context gained primary control of the orientation of the resultant behavior.

The explanation favored here is that the presentation of food to hungry rats activates a general system of response-relevant structures and stimulus sensitivities related to obtaining food (Timberlake, 1983a). With continued presentation of food, local motivational states and specific food-getting behaviors emerge appropriate to the environmental stimuli (see also Leyhausen, 1979). In the case of a rat presented with a ball bearing that reliably predicts food, these behaviors typically include forms of contact with the bearing (predatory and food-handling behaviors), frequently followed by attention to the food tray (focal search and waiting) reflected in digging, sniffing, and attentive waiting. In the case of a rat presented with frequent unpredicted food, the most salient, predictive environmental stimuli are the location of the food delivery, and the rat engages more exclusively in behaviors related to focal search and waiting.

An important aspect of the behavior-system account is the assumption that predatory and focal search behaviors represent two different modes, or strategies, within the feeding system. These two modes are elicited by different circumstances, control different sets of behavior, and are mutually incompatible in that the animal cannot express both modes at the same moment. If food is somewhat uncertain or distant and predation-related cues are present, the animal should display predatory search-and-capture behaviors to the relatively arbitrary stimulus of a moving bearing. With increased certainty of food location and higher food density, animals should show a greater proportion of focal search and waiting.

In the present case, the delivery of unpredicted food pellets produced focal search and waiting at the food tray. When a predictive bearing was introduced, it received attention because of its movement (an important cue in the feeding system) and its proximity to food. However, the development of bearing-directed behavior was interfered with for two reasons. First, the mode of focal search and waiting inhibits the expression and perhaps reduces the

acquisition of behaviors related to a more general search and predation mode. The inhibition of expression is by no means absolute, but appears to occur intermittently on a trial basis. Second, the environmental response contingencies in effect primarily supported food-tray behavior rather than interaction with the bearing. The animal was not required to contact the bearing in order to obtain food, and a food-tray orientation was more efficient than bearing interaction in obtaining food rapidly once it was presented. Thus, neither the environmental contingencies nor the motivational substate supported a change to more predatory behavior. Only the similarity of the moving bearing to a live prey item supported such a change.

It follows from this behavior-system view that the sudden decrease in the probability of food delivery in extinction should decrease the strength of the focal search-and-wait mode, and increase the relative strength of a more general search mode. A more general search mode probably could have been established by other means as well, such as by changing the location of food, by making the food tray less supportive of food-handling behaviors, or by making the bearing more attractive as a predatory cue (a smoothly rolling ball bearing is a rather simple approximation of a moving prey). Any manipulation that changes the relative attractiveness of the food-tray area and the ball bearing or alters other qualities of the environment supporting predation or focal search should alter the behavior shown in the presence of the ball bearing. Once established, a particular form of appetitive behavior should be displaced only by an appropriate combination of decreased support for it and increased support for an alternative food-getting behavior.

In sum, to account for these data, the behavior-system approach appeals to three levels of conditioning: a general state related to obtaining and consuming food; local substates related to particular modes, or strategies, of obtaining food; and specific behaviors oriented to and controlled by environmental stimuli. The strengths of each level interact and are related to the eliciting and supporting qualities of the environment. The results of changes in the conditioning environment will depend on their effects on the instigation and interaction of these levels. In the present circumstances, introducing the predictive bearing was not sufficient to switch the behavior and mode to predation until the interruption of food delivery in extinction produced a further critical increase in the instigation for a more general search mode, while decreasing the instigation for focal search-and-wait behaviors. The result was a relative increase in predatory behavior and a decrease in focal food-tray behavior. With a further decline in the probability of food, activation of the entire feeding system decreased, producing escape and/or quiescence.

Potential Extensions of the Present Approach

Although, in this study, US-alone presentations appeared to interfere with CS-directed behavior primarily at the level of behavioral modes, there is nothing in the behavior-system approach that precludes other sorts of

interference. Because learning is assumed to occur within the context of an evolved functional system, much of the organization and functional control of behavior presumably exists prior to learning. Thus, interference can occur at levels from receiving and processing stimuli through event association to peripheral motor competition for expression.

A disadvantage of this flexibility is that each case of interference must be considered on its own merits. A compensating advantage is that the behavior-system account requires analysis of exactly where and how interference occurs and is expressed. Recent analyses have argued for the existence of multiple-event conditioning at the level of association (e.g., Rescorla, Durlach, & Grau, 1985; Tomie, 1985). The present analysis introduces more complexity by arguing for multiple levels of interference. We may have only begun to touch on the complex determinants of behavioral effects that, until recently, have been attributed to single associative or nonassociative mechanisms (see Bouton & Bolles, 1985; Gibbon & Balsam, 1981; Tomie, 1985).

The possibility of interactions between modes of behavior invites reexamination of some previous examples of context blocking. For example, competition between behavior modes may interfere with autoshaping in pigeons following unpredicted presentations of grain (e.g., Grau & Rescorla, 1984; Tomie, 1981). Timberlake and Lucas (1985) have shown that under short, fixed-time deliveries of food, pigeons develop a relatively stereotyped set of "wall-directed" behaviors, typically involving stepping, bumping with the breast, head bobbing, and neck swinging, against or near the hopper wall (see Innis, Simmelhag-Grant, & Staddon, 1983, for similar data on longer interfood intervals). It could be argued that these behaviors served as an alternative to pecking a lighted key predicting food in the same sense that food-tray behavior in rats was an alternative to bearing-directed behavior. Such a view is supported by the finding of an inverse relation between an activity measure probably related to wall-directed behavior and subsequent autoshaping to a key light (Balsam, 1985; Rescorla et al., 1985).

Similarly, changes in behavioral mode may contribute to the "unblocking" effects of a context shift prior to introduction of the CS. Consider that changing the context alters or eliminates many of the location cues potentially controlling the behaviors conditioned by US-alone presentations. Also, the shift to a novel context may reset the appetitive mode of the subject back toward a more general search pattern. Under this mode, punctate contextual cues (such as a lighted key) should, when used as a predictor, be able to elicit search-related pecking (e.g., Tomie, 1985). A similar shift in mode might explain the recovery in extinction of an autoshaped response that has been eliminated by noncontingent reward (Durlach, 1986; Lindblom & Jenkins, 1981). The noncontingent reward probably more adequately supported a focal search mode

oriented to the hopper rather than autoshaped keypecking; but, in extinction, the animal shifted back to a more general search mode allowing expression of the conditioned keypeck response.

In short, within the behavior-system approach, several manipulations of surprisingness following acquisition, including introduction of moderately novel stimuli and marked reduction in reward, may produce at least a temporary return to a more general search mode. Such a shift should allow performance of conditioned behaviors related to that mode. The possibility of shifts in modes of behavior complicates the presumed basis of phenomena such as blocking (e.g., Pearce and Hall, 1980; Rescorla & Wagner, 1972), and overshadowing (e.g., Matzel, Schachtman, & Miller, 1985).

The behavior-system account also raises some general issues about the nature of extinction and acquisition. In the present data, behavior in extinction appeared to be the result of shifts in the mode of behavior produced by changes in the instigating qualities of the environment. It seems possible to view this as the breaking down of associations between the environment and particular behaviors, but at least in some cases it seems simpler to note that the environment changed and no longer supported a previous mode of behavior. If the environment changed back to support a given mode, its associated behaviors might return rapidly. It may be possible to view acquisition in a similar fashion, as the development of environmental control of successively more specific food-getting modes and related behaviors. In such a view, prior experience with stimulus relations in the conditioning environment could produce modes of behavior that would either abet or interfere with the expression of subsequent conditioning.

In sum, a behavior-system account does not preclude associative interference produced by presentations of the US alone. It does, though, require that an associative analysis be limited and refined by considerations of the animals' evolved appetitive structure. It seems unreasonable that animals should have been selected to make abstract deductions or optimal decisions, store general "information" for some ecologically undefined future use, or control behavior primarily at the level of the strength of a single general associative process. Learning and decision-making typically are based on and occur within existing behavior-system structures.

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(Manuscript received September 30, 1985;
revision accepted for publication April 11, 1986.)