

A Behavior Systems Approach to the Expression of Backward Associations

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In the first phase of Experiment 1 rats were trained with a backward serial conditioned stimulus (CS) with three 8-s elements (Food—Near—Intermediate—Far, where the name of the element denotes its temporal proximity to food). In the second phase of this experiment, different groups received a novel lever presented in compound with a different CS element. In the first phase of Experiment 2, rats were also trained with a similar backward serial CS; but, in the second phase, the entire serial CS was shifted to a forward pairing (Far—Intermediate—Near—Food), and again different groups received a novel lever in compound with a different CS element. In the first phase of Experiment 3, a serial CS was explicitly unpaired with food. The second phase of this experiment was identical to that of Experiment 2. The results showed that lever contact was lowest during the Near element in Experiment 1, highest during the same element in Experiment 2, and indistinguishable among all the elements in Experiment 3. These outcomes support the behavior systems hypothesis that backward CSs come to control a sequence of post-food search modes that can influence subsequent pre-food search. 1998 Academic Press

Most theories of Pavlovian conditioning emphasize the importance of excitatory associations in forward conditioning (when the conditioned stimulus (CS) precedes the unconditioned stimulus (US)) and inhibitory associations in backward conditioning (when the US precedes the CS) (see Hall, 1984; Mackintosh, 1983; Miller & Spear, 1985). The absence of excitatory associations in backward conditioning fits well with the assumption that the function of Pavlovian conditioning is to prepare the organism to interact with an impending US (Hollis, 1982; Mackintosh, 1983; though see Silva, Timberlake, & Koehler, 1996). Because a backward CS never immediately pre-

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cedes an imminent US, it seems unlikely that excitatory responses should be conditioned to a backward CS. Similarly, the presence of inhibitory associations in backward conditioning fits with Rescorla's (1967) contingency analysis of Pavlovian conditioning. According to this view, the negative predictability of the US given the CS should produce a negative association between these stimuli that is below the zero level produced by random CS-US pairings (but see Papini & Bitterman, 1993). An exception to this coherent picture is Wagner's (1981) sometimes opponent process (SOP) theory, which predicts that under conditions of a highly proximal backward CS and a strong US, the CS may control an excitatory conditioned response (CR).

Given this considerable conceptual agreement that backward US-CS pairings should not produce excitatory effects, there is a surprising amount of empirical evidence for such effects (e.g., Albert & Ayres, 1997; Hearst, 1989; Hemmes, Brown, & Cabeza de Vaca, 1994; Keith-Lucas & Guttman, 1975; Matzel, Held, & Miller, 1988; McNish, Betts, Brandon, & Wagner, 1997; Tait & Saladin, 1986; Wagner & Brandon, 1989). Further, it is possible that the reported incidence of excitatory backward learning underestimates this occurrence because most conditioning tests have been based on the assumption that backward excitatory conditioning should be expressed in the form of the same excitatory responses as forward excitatory conditioning (Gallistel, 1990; Miller & Barnet, 1993). Thus, the evidence for the absence of excitatory backward conditioning could be due to the experimenter's choice of a dependent measure rather than to animals' failure to form excitatory associations (Denniston, Miller, & Matute, 1996; Gallistel, 1990; Holland, 1984; Miller & Barnet, 1993; Spetch, Wilkie, & Pinel, 1981).

Are there conceptual frameworks that might help clarify the analysis and measurement of backward excitatory associations? Miller and his collaborators (e.g., Barnet & Miller, 1996; Barnet, Cole, & Miller, 1997; Matzel *et al.*, 1988) have explored the possibility that temporal information between CSs and USs are encoded, preserved, and integrated with the formation of new associations. As a result, an expectation for the temporal location of the US occurs during conditioning trials that follow backward training. The expression of backward excitatory associations depends on the relation of the temporal parameters used during US-CS pairings to those during subsequent conditioning.

In a view more similar to that of Wagner and his associates (Wagner, 1981; Wagner & Brandon, 1989), Timberlake and his collaborators have proposed an ecologically-based framework for the conditioning and expression of excitatory backward associations. For example, Silva *et al.* (1996) examined the possibility that backward conditioning might be understood from a behavior systems approach that considers a species' perceptual sensitivities and response biases related to the US (Domjan, 1994; Fanselow,

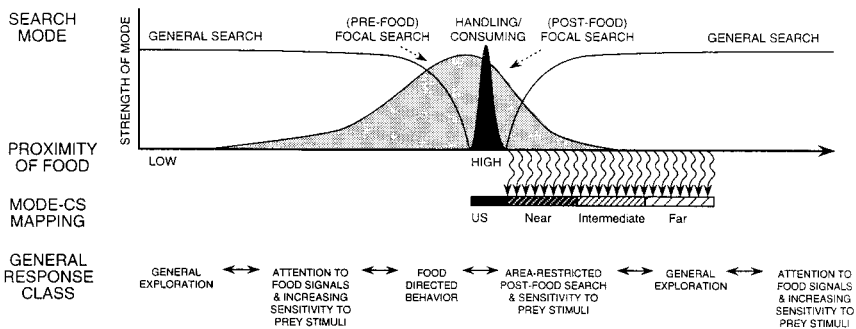


FIG. 1. A representation of the sequence of search modes related to procuring and ingesting food, the associated general response classes, and the mapping between the search modes and stimuli in the environment. Note that with a backward serial CS, the first serial element (Near) is mapped to the post-food focal search mode more than the subsequent elements (Intermediate and Far), which are also mapped to the early stages of general search.

1994; Hogan, 1994; Timberlake, 1983, 1994; Timberlake & Fanselow, 1994; Timberlake & Lucas, 1989; Timberlake & Silva, 1995). According to this approach, the food-finding behavior of a rat is assumed to consist of an organized sequence of perceptual-motor states or search modes related to procuring and ingesting food (see Fig. 1).

In a prototypical sequence, the rat is assumed to begin in a *general search* mode characterized by specific perceptual-motor responses involving attention to novel stimuli and search for specific cues that better predict the location of food. When better predictors are encountered, the animal expresses a *focal search* mode through responses that are more focused on the immediate procurement of food. If food arrives, the animal reveals a *handling/consuming* mode promoting handling and ingestion of the food item. Following ingestion, the animal expresses again a type of focal search mode (*post-food focal search*; see Krebs, 1973; Silva *et al.*, 1996; Whishaw & Gorny, 1991). If more food is rapidly encountered, the animal reenters the handling and consuming mode; otherwise it will return to a general search mode, and then either repeat the cycle or stop foraging. It should be noted that the pre-food focal search mode and the post-food focal search mode are similar (though not identical). The former supports food-anticipatory stimulus sensitivities and responses appropriate to an imminent encounter with food, such as approaching the location where food is likely to be found; the latter supports perceptual-motor responses appropriate to post-food encounters, such as a heightened sensitivity to "escaping" prey and area-restricted search in the region where food has just been eaten.

In relation to Pavlovian conditioning procedures, stimuli present while a

mode is active acquire the capacity, probably through contiguity, to evoke that mode and related responses. Thus, responding during relatively short backward US–CS intervals should be related to post-food focal search mode and the beginnings of a general search mode. Responses more related to general search should emerge with longer US–CS intervals (Silva *et al.*, 1996). For rats receiving a backward serial CS, responses such as nosing in the feeder-area and increased sensitivity to moving objects should be enhanced by the post-food focal search mode conditioned to the serial-elements immediately following food. But the strength of the post-food focal search mode and the accompanying behavioral and perceptual effects should decrease as the time since food passes. In fact, this is what seems to occur (Silva *et al.*, 1996).

The present study used a behavior systems framework to further explore the expression of excitatory backward associations during a serial conditioning procedure. This framework directs us to look for the conditioning and expression of ecologically appropriate perceptual-motor responses appropriate to post- and pre-food focal search modes. The serial procedure allows us to differentiate the temporal stream of search modes following the delivery of the food, and to examine its contribution to subsequent conditioning (e.g., Silva *et al.*, 1996).

In the initial phases of Experiments 1 and 2 of the present study, rats were exposed to a serial CS that followed the delivery of food; in the initial phase of Experiment 3, rats were exposed to a similar serial CS that was explicitly unpaired with food. In the second phase of Experiment 1, a novel lever was compounded with one of the 8-s serial elements. In the second phase of Experiments 2 and 3, the (previously) backward or explicitly unpaired serial CS were shifted to a (now) forward serial CS, and one of the elements was compounded with the lever. In all experiments, contact with a localizable, noisy, moving stimulus such as the lever served as probe for a CS element's capacity to evoke a post-food focal search mode (Silva, 1996; Silva *et al.*, 1996). During the second phase of Experiments 2 and 3 in which a CS element was compounded with a moving lever in a forward conditioning arrangement, nosing in the feeder served as a measure of the pre-food focal search mode.

The purpose of the present study was to test further the hypothesis that backward conditioning with short intervals typically produces a CS that controls an ecologically appropriate post-food focal search mode and related stimulus sensitivities and response tendencies (Silva *et al.*, 1996). In addition, the present experiments sought to clarify Silva *et al.*'s results by examining the effects of their forward test conditions. Briefly, in Silva *et al.*'s study, rats were initially trained with backward pairings of a US and a three-element serial CS. During the subsequent forward test phase, different groups of rats received a (different) single-element of the CS in compound with a

novel lever, and the offset of this stimulus was followed by food. In addition, there were two reinforced presentations of the lever-alone during each of the 12 test sessions to probe the baseline level of responding toward the lever (i.e., to assess how much the rats would contact the lever in the absence of one of the previously conditioned serial elements).

Thus, in their experiment, two aspects of the CS-US relationship changed between the backward serial training phase and the subsequent forward compound test phase: (a) the three-element CS was reduced to a single-element CS, and (b) the US followed the CS rather than preceding it. Second, responding during the serial-element/lever compound may have been affected by reinforced presentations of the lever alone. The combination of altering the sequential configuration of the CS and its temporal relation to the US, and pairing the novel lever alone with the US may have prevented established associations from completely manifesting themselves, or it could have interfered with the development of new associations (Kehoe & Gormezano, 1980; Pearce, 1987; Sutherland & Rudy, 1989). For example, in some conditions, presenting an element of a serial CS in isolation can result in more conditioned responding than is normally elicited by that element when the whole serial CS is presented (Honey, Hall, & Bonardi, 1993).

In the present experiments we maintained the three-element CS in the compound test phase following training and did not present the lever separately from a CS element. Experiment 1 examined the effects of simply adding a lever presentation to one of the elements of a backward serial CS during continued backward pairings. Experiment 2 added lever presentations to one of the elements of a backward serial CS during subsequent forward pairings with the US. Experiment 3 added a lever to one of the elements of an explicitly unpaired serial CS during subsequent forward pairings with the US.

EXPERIMENT 1

According to Silva *et al.* (1996), the temporal distance of a backward serial element from the US should be inversely correlated with the strength of the post-food focal search mode (see Fig. 1). That is, because elements more temporally proximate to food are active at the same time as the asymptote of the post-food focal search mode, these elements should come to control a stronger post-food focal search mode than more temporally remote elements; the latter should be more related to the early stages of a general search mode. Because the animals may still be eating when the first serial element is presented, we expect that nosing in the feeder should be highest in this element, decreasing during the elements of the serial CS further from food (i.e., Near > Intermediate > Far).

In the second phase of the experiment, the rats were divided into three groups and presented with the same backward serial CS, but with one of the serial elements compounded with a novel stimulus (a lever). If serial ele-

ments closer to food have stronger control of a post-food focal search mode than elements farther away, then behavior directed toward the lever should be ordered Group CS_N > Group CS_I > Group CS_F. In a predatory animal like the rat, presenting an auditory moving stimulus such as a lever should trigger approach and manipulation when combined with a serial element controlling post-food focal search provided that no other response competes with approach (Silva *et al.*, 1996).

According to traditional associative theory, backward conditioning should produce inhibitory associations because the CS predicts the absence of the US; however, this depends, to some extent, on the number of US–CS pairings and the preparation (Ayres, Haddad, & Albert, 1987; Hall, 1984; Heth, 1976; Wagner & Terry, 1995). More recent associative theories assume that excitatory backward conditioning may occur during some US–CS intervals (Wagner & Larew, 1985), but designation of the appropriate interval is ambiguous (Janssen, Farley, & Hearst, 1995; but see Barnet *et al.*, 1997). Absent from either analysis is the specification of which CR should be measured when an animal emits multiple CRs. It is unclear *a priori* whether inhibition should predict and be inferred from, for example, a failure to contact the lever, a reduction in nosing in the feeder, or both.

Method

Animals. The animals were 24, female, Sprague-Dawley (*Rattus norvegicus*) rats that were approximately 90 days old at the start of the experiment. The rats were maintained at 85% of their free-feeding weights throughout the course of the experiment, and they were housed in individual cages in a colony room regulated by a 12 h:12 h light:dark cycle. Water was freely available in the home cages.

Apparatus. The apparatus consisted of four metal rectangular boxes (50 × 36 × 32 cm) with a Plexiglas front and top, and an aluminum floor. Each box was contained in a sound-attenuating wood chamber and dimly illuminated by a 25-W light bulb oriented toward the ceiling. A fan located at the back of each chamber provided masking noise and ventilation.

Food pellets (Bio Serv 45-mg dustless pellets, Frenchtown, New Jersey) were delivered by a Waltke Feeder (Bloomington, Indiana) into a metal food tray located in a recessed opening on the back wall of the box. The feeder aperture was 19.5 cm from the right side wall, 15.0 cm from the left side wall, and 5 cm above the floor. An infrared photodetector measured each time a rat placed its head in the food tray. A touch-sensitive retractable lever was located on the left side of the food receptacle, 4 cm from the feeder, 7 cm from the left side wall, and 4.5 cm above the floor. A green jewel light (24-V DC) was located 7 cm above the floor, 3.5 cm from the left of the feeder.

The apparatus was controlled by an IBM-PC and solid state interface located in an adjacent room. Programmed contingencies and data collection

were managed at a 0.1-s resolution, using Conman Contingency Management Software (Spyder Systems, Bloomington, Indiana).

Procedure. Experimental sessions occurred six days a week at approximately the same time each day. Rats were weighed before each session, and, following the session, fed a supplemental amount of food to maintain their weights at 85% ad lib. The rats were fed at the same time on the seventh day. The order of groups was alternated each day to eliminate any time bias. Each session consisted of 12 trials. The interfood interval (IFI) averaged 90 s, with a range between 60 s and 120 s. The experiment preceded through the following stages: chamber adaptation, pretraining (feeder training), serial conditioning, and compound conditioning.

Before actual training took place, each group was placed in the boxes for approximately 20 min to reduce neophobia to the experimental environment. Following this chamber adaptation phase, the rats were feeder trained by placing them in the chambers for a 20-min session during which approximately 24 food pellets (i.e., 2 pellets per trial \times 12 trials) were delivered. On the second day, those rats that did not eat the food on the first day were trained again using the same procedure as the first day.

The backward serial conditioning phase lasted 12 days, and consisted of presenting rats with food, followed by three 8-s elements. The serial element was identified by a subscript that denoted the temporal proximity of an element from the US (Near, Intermediate, Far; abbreviated N, I, or F). Thus, Groups CS_N and CS_F received either a non-flashing light or a light that flashed at a 0.1-s on/off rate. Group CS_I received a light that flashed at a 0.5-s on/off rate. Thus, half the rats received a sequence of lights that flashed faster, and the other half received a sequence that flashed slower, as the time since food elapsed.

Before the start of the compound conditioning phase, the rats were divided into three groups of eight, equated for their ad lib weights. The compound conditioning phase directly followed the backward serial conditioning phase, and was similar to the previous phase except that one of each of the groups received one of the serial-elements in compound with the insertion of the lever. Thus, Groups CS_N, CS_I, and CS_F received the backward serial CS in which the lever was presented in compound with the Near, Intermediate, and Far elements, respectively. Although we expected the effects of the serial backward conditioning to manifest itself early during compound conditioning, we ran this phase for 12 days to monitor any changes in behavior that might occur as a result of presenting the lever with one of the serial-elements. Statistical significance was determined at $p < .05$ for all analyses.

Results and Discussion

Figure 2 shows a progressive decrease in the percentage of trials spent nosing in the feeder across elements of the backward serial CS. An analysis of variance (ANOVA) across 2-day blocks ($N = 24$ rats) showed main ef-

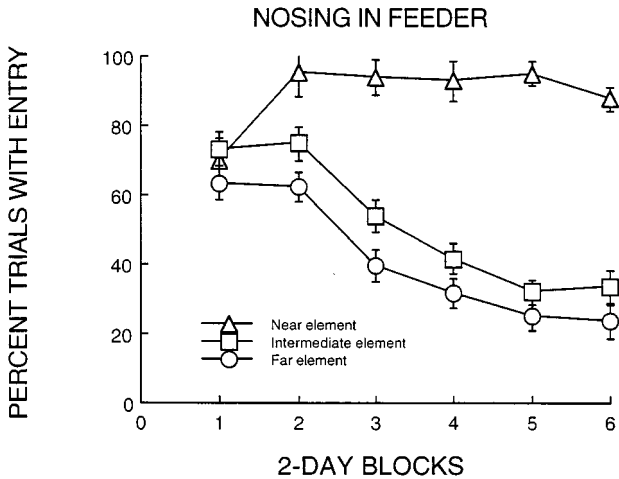


FIG. 2. Percentage (\pm SEM) of trials in which all rats nosed in the feeder during the serial backward conditioning phase in Experiment 1.

fects of element [$F(2, 46) = 191.50$] and days [$F(5, 115) = 14.10$], and an interaction between element and days [$F(10, 230) = 38.70$]. Fishers least significant different (LSD) test confirmed that nosing in the feeder differed between all pairs of elements.

The top graph in Fig. 3 shows the percentage of trials with a lever contact during the compound conditioning phase. Group CS_I showed the most contacts, followed by Groups CS_F and CS_N . An ANOVA across 2-day blocks ($N = 8$ rats per group) showed a main effect of group [$F(2, 21) = 3.84$] and days [$F(5, 105) = 2.51$]. There was no interaction between group and days [$F(10, 105) = .84$]. An LSD test revealed that Group CS_I contacted the lever more than Group CS_N . There were no other statistically significant differences between pairs of groups.

The bottom graph in Fig. 3 shows the percentage of trials in which the rats nosed in the feeder during the compound conditioning phase. Group CS_N nosed in the feeder more than Groups CS_I and CS_F while the lever was presented. An ANOVA across 2-day blocks ($N = 8$ rats per group) showed a main effect of group [$F(2, 21) = 68.70$] and days [$F(5, 105) = 2.31$]. There also was an interaction between group and days [$F(10, 105) = 3.65$]. An lsd test confirmed that Group CS_N nosed in the feeder more than Groups CS_I and CS_F while the lever was available.

The results during backward conditioning showed that nosing in the feeder during the serial CS decreased markedly from the Near to the Intermediate and Far elements. When different elements of the serial CS were compounded with a novel lever, Group CS_I contacted the lever more than Group CS_N . From a behavior systems perspective, elements temporally proximate

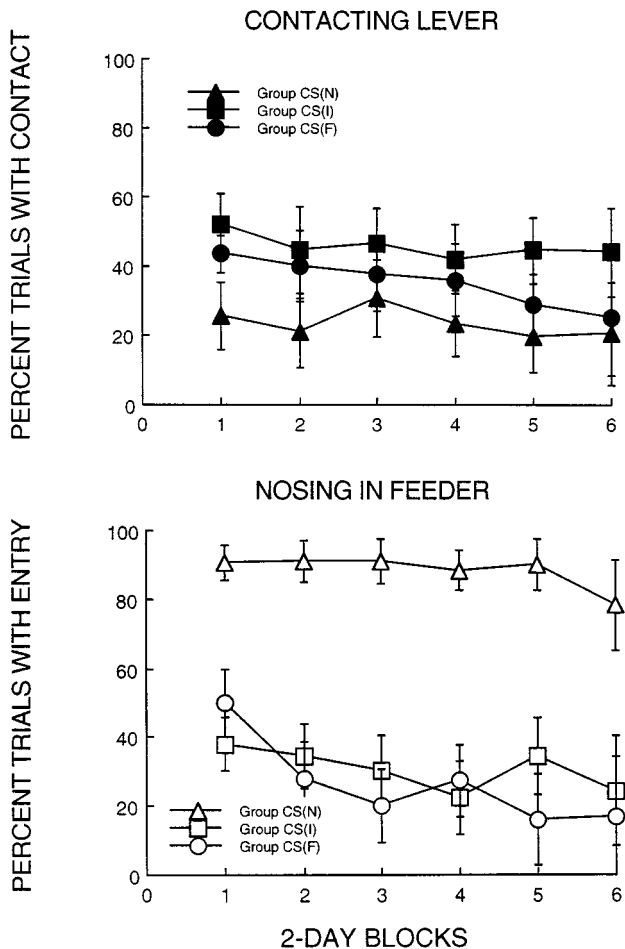


FIG. 3. The top panel shows the percentage (\pm SEM) of trials with a lever contact when the lever was compounded with one of the elements of the serial CS in Experiment 1. The bottom panel shows the percentage of trials (\pm SEM) with an instance of nosing in the feeder when the lever was compounded with one of the elements of the serial CS in Experiment 1.

to the US should be correlated with a stronger post-food focal search mode than more temporally remote elements. When compounded with a moving stimulus, elements evoking a strong post-food focal search mode should have facilitated responding to the moving stimulus. A moving stimulus, such as a lever near the food source, should support handling, biting, and tugging—responses consistent with post-food focal search (Timberlake & Lucas, 1989).

That the serial element most proximate to food did not control the most

lever-directed responding differs from the results of Silva *et al.* (1996), who found that the Near and Intermediate elements supported high levels of lever contact. However, their study differed procedurally from the present experiment in two important ways. First, each element of the backward serial CS was separated from the others before being compounded with the novel lever. Second, each lever and CS-element compound was presented in a forward pairing with food to a separate group of rats (the Near element + lever compound to Group CS_N, the Intermediate element + lever to Group CS_I, and the Far element + lever to Group CS_F). In contrast, in the present study, the backward serial CS remained intact during the compound condition, and the lever was presented in compound with one of the elements in continued backward serial pairings.

Is there a reason why the forward versus backward pairing in the compound condition of these two experiments might make such a difference in lever contact? One possibility is that the backward test procedure in the present experiment allowed responses evoked by presentation of food to interfere with interactions involving the lever during the Near element. Thus, the Near element might still have controlled the strongest post-food focal search mode, but the expression of this mode through lever contact was interfered with by food-evoked nosing in the feeder (see the bottom graph of Fig. 3). A second possibility is that the backward procedure conditioned specific nosing-in-the-feeder responses that interfered with the subsequent attention to the lever. The plausibility of these alternatives can be explored by presenting the backward serial CS in a subsequent forward serial arrangement in which different elements again are compounded with the lever. Because the serial CS and the lever are presented before food, food-evoked nosing in the feeder during the Near element should not compete with lever contact; however, any conditioned nosing-in-the-feeder responses should continue to interfere with lever contact during the Near element.

EXPERIMENT 2

The rats in Experiment 2 were trained with a backward serial CS as in Experiment 1. However, during the test phase, unlike in Experiment 1, the entire backward serial CS was shifted to a forward serial CS, and one of the elements was compounded with the lever. This procedure allowed us to determine whether the low level of lever contact in the test phase of Experiment 1 was due to competition with nosing in the feeder (a) evoked by the US or (b) controlled by the Near element as a result of the backward serial conditioning procedure. If the US evoked nosing in the feeder, then presenting the lever with the Near element during forward pairings of the serial CS and food should not interfere with lever contact. If nosing in the feeder was conditioned to the elements of the backward serial CS, then presenting the lever with the Near element during forward pairings of the serial CS and food should interfere with lever contact.

Method

Animals. The animals were 24, female, Sprague-Dawley rats that were approximately 90 days old at the start of the experiment. The housing conditions were the same as those used in Experiment 1.

Apparatus and procedure. The apparatus, general procedures, and analyses were the same as those used in Experiment 1. The backward serial conditioning phase lasted 12 days, and consisted of presenting rats with food, followed by three 8-s elements. Before the start of the compound conditioning phase, the rats were divided into three groups of eight, equated for their ad lib weights. The compound conditioning phase directly followed the backward serial conditioning phase, and was similar to the previous phase except that one of each of the groups received one of the serial elements in compound with the insertion of the lever, and food followed the CS. Thus, Groups CS_N, CS_I, and CS_F received the (now) forward serial CS in which the lever was presented in compound with the Near, Intermediate, and Far elements, respectively. Although we expected the effects of the serial backward conditioning to manifest themselves early during compound conditioning, we ran this phase for 12 days to monitor any changes in behavior that might occur as a result of presenting the lever with one of the serial-elements in a forward serial conditioning arrangement.

Results and Discussion

Figure 4 shows a progressive decrease in the percentage of trials spent nosing in the feeder across elements of the backward serial CS. An ANOVA

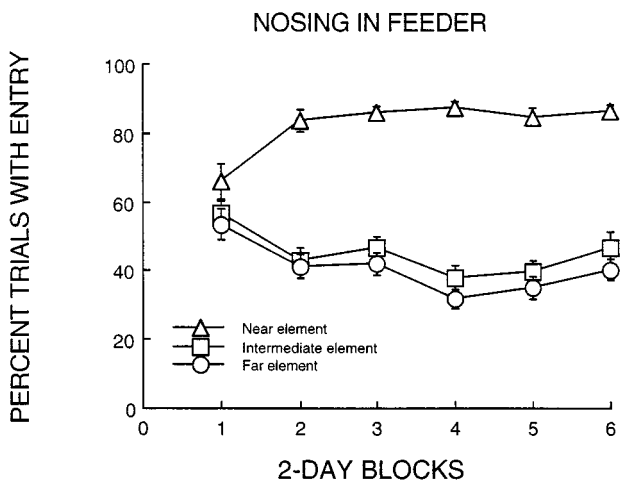


FIG. 4. Percentage of trials (\pm SEM) in which all rats nosed in the feeder during the serial backward conditioning phase in Experiment 2.

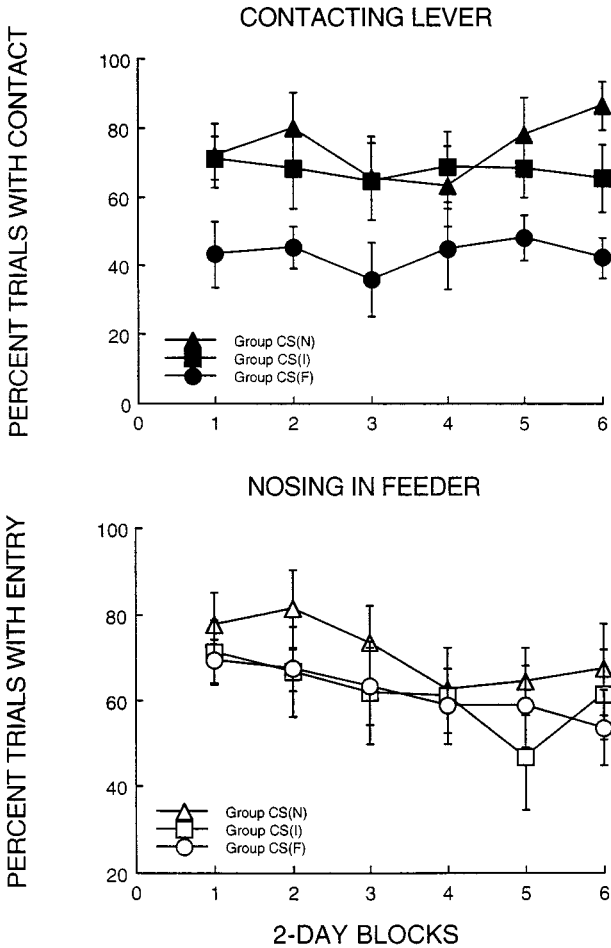


FIG. 5. The top panel shows the percentage of trials (\pm SEM) with a lever contact when the lever was compounded with one of the elements of the (now) forward serial CS in Experiment 2. The bottom panel shows the percentage of trials (\pm SEM) with an instance of nosing in the feeder when the lever was compounded with one of the elements of the (now) forward serial CS in Experiment 2.

across 2-day blocks ($N = 24$ rats) showed main effects of element [$F(2, 46) = 105.58$] and days [$F(5, 115) = 12.06$], and an interaction between element and days [$F(10, 230) = 10.39$]. An LSD test confirmed that nosing in the feeder differed between all pairs of elements.

The top graph in Fig. 5 shows the percentage of trials with a lever contact during the compound conditioning phase. Groups CS_N and CS_I showed the

most contacts, and Group CS_F showed the fewest contacts. An ANOVA across 2-day blocks ($N = 8$ rats per group) showed a main effect of group [$F(2, 21) = 3.66$], but no effect of days [$F(5, 105) = 1.42$] nor an interaction between group and days [$F(10, 105) = .67$]. An LSD test confirmed that Group CS_N contacted the lever more than Group CS_F.

The bottom graph in Fig. 5 shows the percentage of trials in which the rats nosed in the feeder during the forward compound conditioning phase. There appears to be an decrease across days, but no differences between the groups. An ANOVA across 2-day blocks ($N = 8$ rats per group) showed no main effect of group [$F(2, 21) = .46$], but a significant effect of days [$F(5, 105) = 4.55$]. There was no interaction between group and days [$F(10, 105) = .52$].

The results during initial backward training showed that nosing in the feeder during the serial CS decreased markedly from the Near to the Intermediate and Far elements. When different elements of the serial CS were compounded with a novel lever, Group CS_N contacted the lever more than Group CS_F. These effects are consistent with the behavior systems view that backward-paired elements temporally proximate to the US should be correlated with a stronger post-food focal search mode than more temporally remote elements. When compounded with a moving cue, elements evoking a strong post-food focal search mode should facilitate responding to the moving lever.

Although the results of Experiment 2 are consistent with a behavior systems account, it is possible to argue that the outcome resulted from the forward procedure of Phase 2 rather than the backward serial procedure in Phase 1. However, for two reasons, this seems unlikely. First, despite two major procedural differences between the present experiment and Silva *et al.*'s (1996) study, the results of the two experiments are nearly identical. Recall from the Introduction that, in Silva *et al.*'s study, the elements of the backward serial CS were separated and presented individually with the lever in a forward compound arrangement. Moreover, they presented two reinforced trials of the lever alone during each of their test sessions. Despite these differences, the Near and Intermediate elements in both Silva *et al.*'s study and the present experiment supported high levels of lever-directed behavior. If the results of Experiment 2 were solely the outcome of pairings during Phase 2, then the results should have been different from Silva *et al.*'s.

Second, the greater amounts of lever contact displayed by Groups CS_N and CS_I are inconsistent with what is observed when Phase 1 consists of forward rather than backward serial conditioning. Following forward serial training, rats show the greatest lever contact during the Far, not Near, element (Silva *et al.*, 1996). In addition, manipulation responses such as contacting a lever or rolling ball-bearing tend to occur at longer CS-US intervals. Presentations of these stimuli close to the delivery of food causes them to evoke feeder-rather than CS-directed behavior (Timberlake *et al.*, 1982). If the re-

sults of Experiment 2 were solely the outcome of Phase 2, then we would have expected more lever contact during the Far and Intermediate elements than the Near element.

EXPERIMENT 3

Taken together with the results of Silva *et al.* (1996), the outcome of Experiment 2 supports the view that serial backward training results in the conditioning of search modes. Nevertheless, Experiment 3 attempted to directly evaluate the possibility that the differential amounts of lever contact observed in Experiment 2 were solely the result of forward conditioning in Phase 2.

The rats in Experiment 3 were initially trained with a serial CS that was explicitly unpaired with the food. This procedure allowed us to present the same number of serial CSs and USs as those presented in Experiment 2. During the second phase, as in Experiment 2, the entire serial CS was shifted to a forward serial CS, and one of the elements was compounded with the lever. Because the serial CS occurs in the middle of the IFI and is explicitly unpaired with the US, no element should differentially control nosing in the feeder during initial training nor contacting the lever during the subsequent forward pairings in the test phase (i.e., Group CS_F = Group CS_I = Group CS_N). However, if no conditioning occurred in the backward serial training phase of Experiment 2, and the results of that experiment were due solely to the forward serial conditioning of the test phase, then we would expect the results of Experiment 3 to look like those of Experiment 2. Lever contact should be highest during the Near element and least during the Far element (i.e., Group CS_N > Group CS_I > Group CS_F).

It is worth noting that presenting explicitly unpaired stimuli is viewed rather differently by traditional associative theory and the behavior systems account. In the traditional view, unpaired presentations should condition inhibition to the serial CS. In the behavior systems view, unpaired presentations should condition more of a general search mode (see Fig. 1). Responses appropriate to the general search mode include a reactivity to moving objects such as a lever (Silva *et al.*, 1996) or ball-bearing (Silva, 1996; Silva & Timberlake, 1997; Timberlake *et al.*, 1982). Thus, relative to the results of Experiment 2, the traditional associative view might expect considerably lower levels of responding to the lever in the forward pairing phase of the present experiment. In contrast, the behavior systems view would expect the same or higher levels of responding to the lever.

Method

Animals. The animals were 24, female, Sprague-Dawley rats that were approximately 90 days old at the start of the experiment. The housing conditions were the same as those used in Experiment 1.

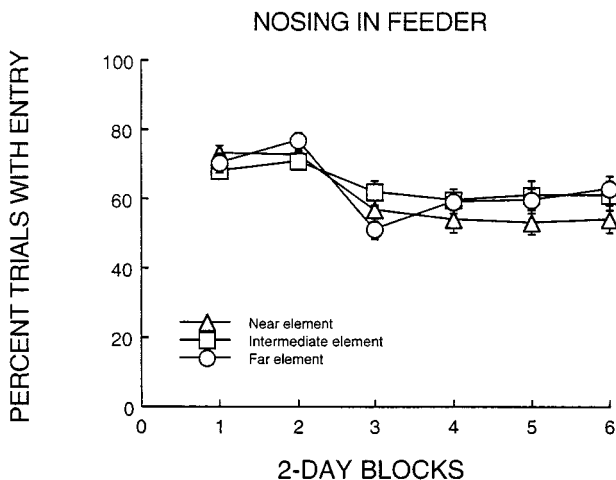


FIG. 6. Percentage of trials (\pm SEM) in which all rats nosed in the feeder during the explicitly unpaired serial conditioning phase in Experiment 3.

Apparatus and procedure. The apparatus, general procedures, and analyses were the same as those used in Experiment 1. The explicitly unpaired serial conditioning phase lasted 12 days, and consisted of presenting rats with the three 8-s element serial CS in the middle of the IFI. Food was presented at the end of the IFI. In an explicitly unpaired situation, the designation of an element's temporal proximity to the US can be referenced to the time following or preceding the US. To be consistent with the previous experiments, the Near, Intermediate, and Far elements during Phase 1 denoted the temporal proximity of an element from the US following the presentation of the US. Before the start of the forward compound conditioning phase, the rats were divided into three groups of eight, equated for their ad lib weights. The forward compound conditioning phase (identical to that of Phase 2 of Experiment 2) directly followed the serial conditioning phase, and consisted of presenting one of each of the groups with one of the serial-elements in compound with the insertion of the lever. Food followed the CS. Thus, Groups CS_N , CS_I , and CS_F received the forward serial CS in which the lever was presented in compound with the Near, Intermediate, and Far elements, respectively. We ran this phase for 12 days to monitor any changes in behavior that might occur as a result of presenting the lever with one of the serial elements in a forward serial conditioning arrangement.

Results and Discussion

Figure 6 suggests that there was no difference in the percentage of trials spent nosing in the feeder across elements of the explicitly unpaired serial CS. However, a repeated measures ANOVA ($N = 24$ rats) across 2-day

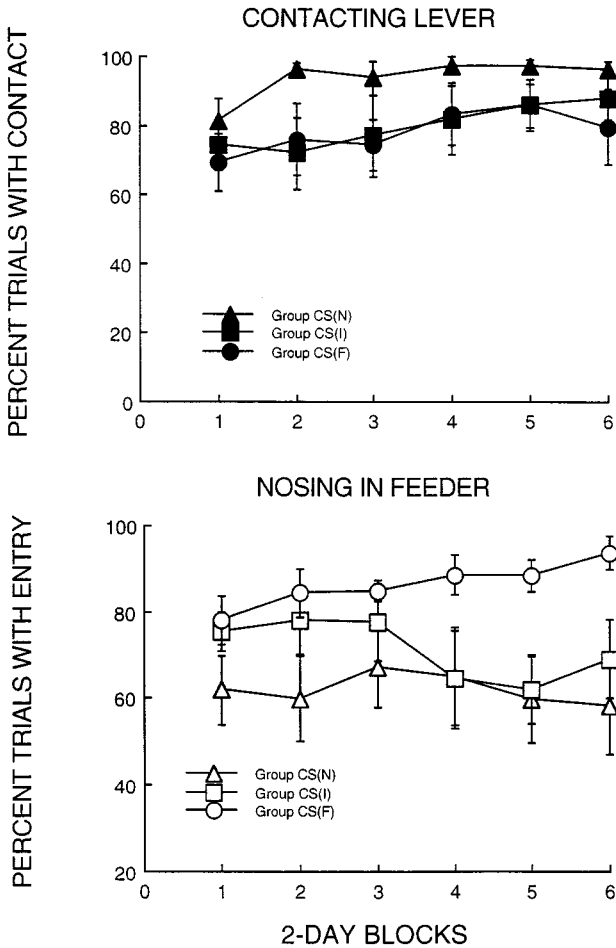


FIG. 7. The top panel shows the percentage of trials (\pm SEM) with a lever contact when the lever was compounded with one of the elements of the (now) forward serial CS in Experiment 3. The bottom panel shows the percentage of trials (\pm SEM) with an instance of nosing in the feeder when the lever was compounded with one of the elements of the (now) forward serial CS in Experiment 3.

blocks revealed that there was a main effect of element [$F(2, 46) = 6.52$], days [$F(5, 155) = 11.08$], and an interaction between element and days [$F(10, 230) = 2.99$]. An LSD test revealed that there was a small but reliable tendency to check the feeder less as serial-elements were presented. The overall average percentage of trials with an instance of nosing in the feeder was 64.9%, 62.9%, and 60.1% across the Near, Intermediate, and Far elements, respectively, of the serial CS.

The top graph in Fig. 7 shows the percentage of trials with a lever contact

during the compound conditioning phase. On some days, Group CS_N appears to contact the lever slightly more than the other groups. However, an ANOVA across 2-day blocks ($N = 8$ rats per group) showed that there was no main effect of group [$F(2, 21) = 1.52$]. There was an effect of days [$F(5, 105) = 7.27$], but no interaction between group and days [$F(10, 105) = 1.00$].

The bottom graph in Fig. 7 shows the percentage of trials in which the rats nosed in the feeder during the compound conditioning phase. It appears that Group CS_F nosed in the feeder more than Groups CS_I and CS_N . An ANOVA across 2-day blocks ($N = 8$ rats per group) confirmed that there was a main effect of group [$F(2, 21) = 3.49$], but no effect of days [$F(5, 105) = .54$], nor an interaction between group and days [$F(10, 105) = .19$]. An LSD test confirmed only that Group CS_F nosed in the feeder more than Group CS_N .

The results during explicitly unpaired serial training showed that nosing in the feeder decreased slightly across elements of the serial CS. However, when different elements of the serial CS were compounded with a novel lever, all elements supported similar, high levels of lever contact (i.e., Group $CS_F =$ Group $CS_I =$ Group CS_N). These effects are consistent with the view that different amounts of lever contacts in Experiment 2 were due to the backward serial training, and that the serial CS in Experiment 3 came to control the middle stages of a general search mode.

GENERAL DISCUSSION

This research explored the expression of excitatory backward associations from a behavior systems approach. In the acquisition phase of Experiments 1 and 2, rats were trained with a backward serial CS (Food—Near—Intermediate—Far) consisting of 8-s elements. During a subsequent backward (Experiment 1) or forward (Experiment 2) compound conditioning phase, different subgroups of rats received the same serial CS with one of the elements compounded with a novel lever.

The results during backward conditioning showed that nosing in the feeder during the serial CS decreased markedly from the Near to the Intermediate and Far elements. When different elements of the serial CS were paired with a novel lever in a backward compound condition, Group CS_N contacted the lever less than Group CS_F . However, when the different elements of the serial CS were paired with the lever in a forward compound condition, Group CS_N contacted the lever more than Group CS_F .

The results supported the use of a behavior systems framework for analyzing excitatory backward conditioning. According to this view, the US anchors the end of a sequence of pre-food focal search and the beginning of a sequence of post-food focal search. In terms of post-food focal search, serial elements proximate to the US should come to control aspects of search behavior selected for their likelihood in finding other food. One aspect is a

sensitivity to stimuli that possess some characteristics of prey, such as sound or movement. Thus, maximal contact with a nearby lever should occur when its presentation is compounded with a stimulus controlling a post-food focal search mode. More distant serial elements should come to control the early stages of a general search mode, which should be less sensitive to immediate prey stimuli.

A second finding was evidence of competition for expression between food-related responses (nosing in the feeder) and contacting the lever when a novel lever was presented as part of a backward serial CS following food, but not when it was part of the same serial CS presented before food. During backward compound conditioning, there was more lever contact during the Intermediate and Far elements than during the Near element. During forward compound conditioning, there was more lever contact during the Near and Intermediate elements than during the Far element. A ready interpretation of these results was that ingesting the food interfered with the expression of lever contact when the Near element followed food (cf. Fig. 3). Shifting the backward serial CS so that it occurred before the presentation of food allowed the Near element to evoke a strong post-food focal search mode conditioned in the previous phase, and for the expression of this mode in terms of lever contact.

Experiment 3, in which a serial CS was explicitly unpaired with food, addressed the possibility that the different amounts of lever contact in Experiment 2 were the result of forward serial conditioning rather than the previous backward serial conditioning. If no conditioning occurred during the backward serial conditioning phase of Experiment 2, then the results of Experiment 3 should have looked like those of Experiment 2 in which lever contact was highest during the Near element and least during the Far element (i.e., $\text{Group CS}_N > \text{Group CS}_I > \text{Group CS}_F$). This did not occur. In Experiment 3, there was no differential control of lever contact when elements of the (previously) explicitly unpaired serial CS were compounded with the lever in a (now) forward conditioning arrangement, though all elements controlled substantial levels of lever contact. This effect is consistent with the behavior systems view that a serial CS explicitly unpaired with food should come to control the middle stages of a general search mode. When compounded with a moving stimulus, elements evoking the middle stages of a general search mode should facilitate responding to noisy, punctate, moving stimuli, such as a lever (Timberlake, 1994; Timberlake & Lucas, 1989; Timberlake & Silva, 1995).

The results of the present experiments are consistent with a behavior systems account that backward serial training results in the conditioning of search modes. These outcomes also may be compatible with some contemporary associative theories such as SOP and its affective-emotional extension, AESOP, which suggest that each element of a backward serial CS should acquire its own associative strength in relation to its temporal proximity of

the US (Wagner, 1981; Wagner & Brandon, 1989), thereby allowing for excitatory associations. It is still unclear, though, which US–CS intervals should produce excitatory and inhibitory associations (Janssen *et al.*, 1995; Wagner & Larew, 1985), or how many pairings are needed for excitatory associations (e.g., see Albert & Ayres, 1997). Despite this ambiguity, AESOP's distinction between affective and sensory processes may have parallels with the distinction between the conditioning of different search modes.

Traditional associative theories appear to have more difficulties with the present results because they have no principles specifying *a priori* which CRs should be measured, why they should be measured, or how changes in these CRs should be interpreted. Thus, if we assume that nosing in the feeder during initial training reflects the associative strength of the serial element, then it is still unclear how a purely associative view would aid in the analysis of subsequent conditioning. For example, in forward compound conditioning, when an element of the serial CS was presented with the lever, a blocking explanation could predict that the strongest elicitor (Near) should block responding to the lever more than the weakest elicitor (Far). The results of Experiment 1 appear potentially consistent with this view, but those of Experiment 2 and Silva *et al.* (1996) do not. Perhaps what is needed to understand the role of traditional associative variables is a more complex research design consisting of unpaired, randomly paired, and no treatment control groups. These latter groups would allow us to evaluate whether lever contacts in Experiment 2 were elevated above a neutral baseline, a possibly inhibitory baseline, or an excitatory baseline.

Still, even with the addition of more control groups, a traditional associative view does not specify which response should be used to assess the role of blocking or inhibition, and exactly how the two CRs, nosing in the feeder and contacting the lever, should interact. Traditional associative constructs are most useful and easily applied when the analysis of the behavioral outcome is restricted to a single CR (Silva *et al.*, 1996; Timberlake & Silva, 1994). What seems to be lacking is a conceptual specification of how to translate constructs rooted in associative strength into a multi-response output.

We do not intend to argue here that traditional associative constructs could not be used to explain the present results. Neither the behavior systems view nor the present experiments were designed to rule out the contribution of associative variables (see also Suboski, 1990; Timberlake, 1994). However, there are some procedural and conceptual assumptions that appear to be worth reconsidering. The apparent presence or absence of excitatory backward associations seems to be linked closely to experimenter's choice of responses and the circumstances used to assay these associations (see also Denniston *et al.*, 1996; Holland, 1984; Miller & Barnet, 1993; Matzel *et al.*, 1988; Tait & Saladin, 1986). The present results suggest that the behavior

systems approach, with its attendant focus on organized modes of stimulus sensitivities and responses, can help clarify the nature of backward conditioning, how it is controlled, and how it should be measured (Silva *et al.*, 1996; Timberlake & Silva, 1994).

The analysis of issues such as the temporal course of conditioning, the effect of compounding serial-elements with a moving stimulus, and the dynamics of competing responses may be facilitated by placing the conditioning of associations within a behavior systems framework (Timberlake, 1994). The behavior systems approach predicts the expression of CRs by assuming that responding should follow a natural foraging sequence (Timberlake & Silva, 1995). Animals should engage in the most appropriate responses from their repertoire based on the physical characteristics of the CS and US and their spatial and temporal arrangement. In this view, the relative strength of different responses is not tied directly to associative strength. Instead, emergent responses reflect interactions among different search modes or competition within them (Timberlake, 1986).

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