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The influence of the information value provided by prior-cuing treatment on the reactivation of memory in preweanling rats

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In two experiments, the influence of exposure to a CS− on the acquisition and retention of a conditioned odor aversion was examined. Preweanling rats were given exposure to the CS− either prior to (CS−/CS+) or following (CS+/CS−) the pairing of a second odor (the CS+) with footshock. The results of Experiment 1 indicated that subjects in both of the treatment conditions acquired aversions of comparable strength to the odor paired with footshock and that retention of the odor aversion was not affected by order of stimulus presentation during conditioning. Experiment 2 indicated, however, that the effectiveness of pretest exposure to various elements of the conditioning episode in reactivation of the memory for conditioning *was* dependent on the order of stimulus presentation during conditioning. This differential effectiveness of the various reactivation treatments is discussed in terms of their relationship to the associative "status" of the stimuli present during conditioning and in terms of the information provided to the animal by the reactivation treatment.

Apparent age-related differences in learning rate may be largely a consequence of age-related changes in stimulus selection—what is learned from among the many elements and relationships that could be learned in a particular episode. Ontogenetic differences in stimulus selection are evident in a variety of circumstances (for reviews, see Spear & Kucharski, 1984a, 1984b; Spear, Kucharski, & Miller, 1989), including a tendency for younger animals to show greater conditioning to "incidental" stimuli present at the time of conditioning. For example, Solheim, Hensler, and Spear (1980) found that a shift in the context from training to testing resulted in a disruption in the performance of active avoidance in young animals that was not evident in adults. Using a Pavlovian conditioning procedure, Lariviere, Chen, and Spear (1990) gave rats pairings of a black chamber and footshock in the presence of an olfactory contextual cue and also exposed them to a white chamber and no footshock in the presence of the same odor; that is, the odor was present during CS+ and CS− presentations. Although the adult and preweanling animals acquired an equivalent aversion to the black chamber, the preweanling subjects also acquired an aversion to the olfactory context that the adult animals did not acquire. It appears that, relative to adults, preweanlings are more likely to express conditioning to all elements present during training and less likely to single out the CS+ as the element that best predicts the unconditioned stimulus (US).

A factor that has been shown to facilitate the preweanling's conditioning to a target CS is the presence of a CS− (a second stimulus, from the same dimension as the CS+, that is not paired with footshock) at the time of conditioning. This factor has been studied recently in a series of experiments examining the effect of exposure to a CS− on preweanling rats tested in a one-trial conditioning procedure (Miller, Jagielo, Gisquet-Verrier, & Spear, 1989; Miller, Jagielo, & Spear, 1989; Miller & Spear, 1989). Some rat pups were given a CS+ alone paired with footshock, and others were given exposure to a CS− prior to the CS+/footshock pairing (the CS−/CS+ procedure). The typical pattern of results from those studies was that during the first 2 postnatal weeks, pups conditioned with both the CS− and CS+ expressed an aversion to the stimulus that was paired with footshock, but pups conditioned with the CS+ alone did not.

These studies accumulated a reasonable amount of evidence indicating that CS− exposure facilitates the *acquisition* of the conditioned aversion. We became interested

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in the possibility that CS− exposure might also influence the animal's retention of conditioning. The opportunity to study the effect on retention independently of the effect on acquisition arose from the discovery that whereas exposure to the CS− was necessary for conditioning in 8- and 12-day-old rats, 18-day-old animals expressed similar conditioning with or without CS− exposure. This finding with the 18-day-old rat provided the opportunity to examine the effect of the CS− on retention without contamination by differences in the initial strength of the conditioning.

Retention by 18-day-old rats conditioned with the CS−/CS+ procedure or with the CS+ alone was assessed with a preference test between the CS+ and a novel nonpreferred odorant or between the CS+ and the CS− (Miller, Jagielo, & Spear, 1990). The results indicated that presence of the CS− during conditioning facilitated later retention of the conditioned aversion, but only if the CS− was also present at the time of testing. These results suggested that the CS− might enhance retention by serving as a retrieval cue at the time of testing. Support for this notion was provided by subsequent experiments using a prior-cuing procedure. Different groups of subjects were exposed to various elements of the conditioning episode prior to testing. Pretest exposure to the CS−, as well as to either the conditioning context or to the US, resulted in the expression of conditioning that was not evident in the absence of a prior-cuing treatment. The extreme effectiveness of the CS− as a retrieval cue was somewhat surprising, particularly in contrast to the ineffectiveness of other salient elements of the conditioning episode as prior-cuing treatments (e.g., the CS+).

One possible reason why the CS− serves as an extremely effective retrieval cue is that it had preceded—predicted—the pairing of the CS+ and the US in the same way as stimuli that serve an "occasion-setting" function (e.g., Holland, 1983, 1986), although the training procedures typically used to produce an effective occasion-setting stimulus are quite different from the one-trial conditioning procedure used in the present studies. If the extreme effectiveness of the CS− as a prior-cuing stimulus is ultimately linked to its unique ability to signal the pairing of the CS+ and the US, one would expect the CS− to serve as an effective reactivation treatment if it precedes the pairing of CS+ and US during conditioning, but not if it follows the pairing. The present experiments provide an initial test of this occasion-setting hypothesis by varying the order of stimulus presentation during training and subsequently examining the influence of pretest exposure to the CS− on retention.

EXPERIMENT 1

To examine the influence of the order of stimulus presentation on the effectiveness of the CS− as a prior-cuing treatment, it is necessary to establish with comparable procedures that presentation of the CS− prior to conditioning results in the same amount of conditioning as does presentation of the CS− following the CS-US pairing, so that differences in retention will not be confounded with differences in the strength of initial acquisition.

Method

Subjects. The subjects were 40 18-day-old naive Sprague-Dawley-derived male and female rats from our breeding colony at SUNY Binghamton. The subjects were housed with both parents and conspecifics until experimentation. All subjects were maintained in a climate-controlled colony room with a 16:8-h light:dark cycle, with light onset at 0700 h.

Apparatus. Conditioning took place in a clear Plexiglas chamber (10.16 × 15.24 × 20.32 cm) with a grid floor. The grid floor was made of stainless steel rods (2 mm in diameter), with a 4-mm separation between the rods. The odorants used as CSs were placed on cotton underneath the grid floor of the conditioning chamber. The CS+ was 2.0 cc of methyl salicylate (Aldrich Chemical) and the CS− (located in a different room from the CS+) was 1.0 cc of lemon oil (Humco). The time required to transport the subjects from the CS− to the CS+ was approximately 10 sec. Preference testing, which took place in a room located away from where the CS+ and CS− were presented, was conducted in a clear Plexiglas chamber (27.94 × 10.64 × 12.38 cm), with a layer of clean shavings on the chamber floor. The CS+ (2.0 cc of methyl salicylate) was spread on a cotton-covered roller inserted into an 8.5 × 2.5 cm opening located 13 mm above the floor at one end of the preference-testing chamber, and the alternative odor (.75 cc of orange oil; Humco) was spread on a cotton-covered roller inserted into an opening at the opposite end of the chamber (previous studies in our laboratory indicated that untreated subjects demonstrate a preference for the methyl odor). The holding cage was a standard opaque maternity cage divided into eight compartments containing clean shavings. Footshock was delivered via a Grason-Stadler shock generator (Model E1064GS).

Procedure. Each treatment condition was made up of 10 animals (4–6 animals of each sex/group) and included subjects from a minimum of five litters per condition. Prior to conditioning, each subject was placed into an individual compartment in the holding cage. The subjects in the CS−/CS+ condition were then placed in the compartment holding the lemon odor (CS−) for 30 sec. Following this exposure, the subjects were placed in the compartment holding the methyl odor (CS+) for 30 sec. A 3-sec, 1.6-mA scrambled footshock was delivered at the beginning of Seconds 8, 18, and 28 of this placement. The subjects in the CS+/CS− condition were treated similarly except that they were placed in the lemon odor following the methyl-footshock pairing. The subjects in the unpaired control groups (included for each treatment condition) received their footshock 20 min prior to CS exposure, during a 30-sec placement in a clear Plexiglas chamber in which no odorants were added.

Following conditioning treatments, the subjects were given a preference test between the methyl and orange odors. At the beginning of the preference test, each subject was placed in a position so that it faced a side wall at the center line that divided the test chamber. Positioning of the rat's snout across the midline was the criterion used for entry into a compartment. An observer, unaware of each animal's conditioning treatment, recorded time spent on the methyl side of the chamber during a 60-sec test period.

Results and Discussion

The results of the preference test are presented in Figure 1. A 2 (paired vs. unpaired) × 2 (order of stimulus presentation) analysis of variance (ANOVA) indicated a significant main effect of the paired versus unpaired treatment condition(s) [$F(1,36) = 200.57$, $p < .01$]. The

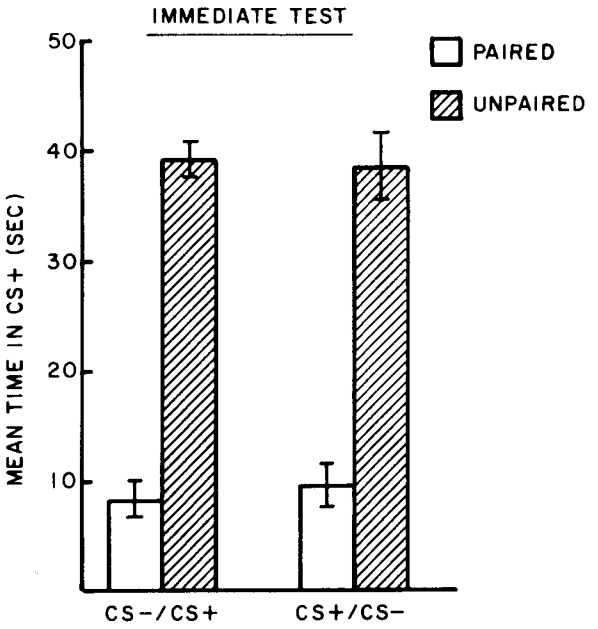

Figure 1. Mean seconds spent in CS+ by subjects given CS− exposure prior to (CS−/CS+) or following (CS+/CS−) the pairing of methyl odor with footshock. (Vertical lines indicate standard errors of the mean.)

main effects of the order of stimulus presentation [$F(1,36) = .20$] and the interaction [$F(1,36) = .18$] were not significant. Post hoc comparisons were conducted using the Fisher test (Keppel, 1982) with the significance level set at $p < .05$. Pairwise comparisons indicated that paired subjects in both the CS−/CS+ and CS+/CS− treatment conditions spent significantly less time in the CS+ than did the subjects in their respective unpaired control conditions, indicating acquisition of the conditioned odor aversion. There was no significant difference in time spent in the CS+ by paired subjects in the two stimulus-presentation conditions, indicating that the strength of the conditioned odor aversion was comparable regardless of whether the CS− preceded or followed the CS+/footshock pairing. Finally, there was no significant difference between the subjects in the two unpaired control conditions.

These results indicated that the subjects acquired an aversion to the odor that was paired with footshock. The strength of this conditioning was not differentially affected by whether exposure to the CS− preceded or followed pairing of the CS+ and US.

EXPERIMENT 2

The results of Experiment 1 indicated comparable levels of conditioning in the subjects conditioned with the CS−/CS+ and CS+/CS− procedures. These procedures allowed examination of the reactivation of memory following conditioning with either order of stimulus presentation, without confounding by differences in the strength of initial conditioning. In Experiment 2, the reactivation of memory was examined following pretest exposure to a variety of prior-cuing procedures. The general hypothesis was that the information provided by the CS− determines its effectiveness as a prior-cuing treatment (Miller, Jagielo, & Spear, 1990, 1991). In all of our previous tests, exposure to the CS− had always preceded the pairing of the CS+ and US, perhaps providing information to the animal about the "status" of the CS+ (i.e., that the stimulus will be followed by the US). If this information provided by the CS− is critical to its role as an effective reactivation treatment, then we would not expect the CS− to serve as an effective prior-cuing treatment for those subjects that, during conditioning, had received CS− exposure *after* the pairing of the CS+ and US.

Retrieval of a target memory may depend not only on the information value provided by a prior-cuing treatment, but also on the number of retrieval cues available to the animal. A further purpose of Experiment 2 was to examine the prior-cuing effect of a novel combination of single elements of the conditioning episode that were previously known to serve individually as effective reactivation treatments. Two elements of the conditioning episode that we have routinely found to be effective in facilitating retrieval of the target memory have been pretest exposure to either the CS− or the US. In these previous studies, prior cuing with the US has always occurred in the same room where the pairing of the CS+ and US was delivered. To examine the effectiveness of the CS− and US in combination as a reactivation treatment, it is necessary to verify that administration of the US does not become ineffective as a prior-cuing treatment when pretest exposure to that cue occurs in the context where the CS− is presented during training. The present experiment examines the effectiveness of prior cuing with either the US alone (delivered in the context where the CS− is presented during training), the CS− alone, or the CS− and US combined as reactivation treatments following conditioning with either the CS−/CS+ or CS+/CS− procedure.

Method

Subjects. The subjects were 160 18-day-old naive Sprague-Dawley-derived male and female rats reared and housed as described previously.

Apparatus. The apparatus and odorants used as conditioned and test stimuli were as described previously.

Procedure. Each treatment condition was made up of 10 animals (4-6 animals of each sex/group) and included subjects from a minimum of five litters per condition. Prior to conditioning, each subject was placed into an individual compartment in the holding cage. The subjects in the CS−/CS+ condition were then placed in the compartment holding the lemon odor (CS−) for 30 sec. Following this exposure, the subjects were placed in the compartment holding the methyl odor (CS+) for 30 sec. A 3-sec, 1.6-mA scrambled footshock was delivered at the beginning of Seconds 8, 18, and 28 of this placement. The subjects in the CS+/CS− condition were treated similarly except that they were placed in the lemon odor following the methyl-footshock pairing. The subjects in the unpaired control groups (included for each treatment condition)

received their footshock 20 min prior to CS exposure, during a 30-sec placement in a clear Plexiglas chamber in which no odorants were added.

Following the conditioning treatments, the subjects were each placed into an individual compartment in the holding cage for a 3-h retention interval (this retention interval was chosen on the basis of previous data indicating that forgetting is complete, that is, the aversion is no longer expressed, at this postconditioning interval when the current one-trial conditioning procedure is used; Miller, Jagielo, & Spear, 1989, 1990, 1991). Five minutes prior to the end of the retention interval, the subjects in each of the three prior-cuing treatment conditions were given a 30-sec exposure to a selected element(s) of the training episode.

The prior-cuing treatments were (1) the US used during training (30-sec placement into a nonodorized chamber in the same room where CS− exposure occurred, with footshock beginning at sec 8, sec 18, and sec 28 of this placement); (2) the CS− used during training; or (3) placement into the CS− used during training, with footshock delivered at Seconds 8, 18, and 28 of this placement (CS− and US combined). Immediately following the prior-cuing treatment, the subjects were returned to the holding cage for the remainder of the retention interval. The subjects in the no-prior-cuing treatment condition remained in the holding cage undisturbed for the entire retention interval. At the end of the retention interval, all subjects were given a preference test between the methyl and (novel) orange odors, as described previously.

Results and Discussion

The results of the preference test are presented in Figure 2. A 2 (paired vs. unpaired) × 2 (order of stimulus presentation) × 4 (prior-cuing treatment) ANOVA indicated a significant main effect of the paired versus unpaired treatment conditions [$F(1,144) = 168.46, p < .01$], a significant main effect of the prior-cuing treatment [$F(3,144) = 14.67$, $p < .01$], and a significant interaction between the paired versus unpaired treatments and the prior-cuing treatment [$F(3,144) = 13.51, p < .01$]. The main effect of the order of stimulus presentation [$F(1,144) = .40$], the interaction between the paired versus unpaired treatment conditions and the order of stimulus presentation [$F(3,144) = .79$], the interaction between the order of stimulus presentation and prior-cuing treatment [$F(3,144) = 1.91$], and the three-way interaction [$F(3,144) = 2.20$] were all nonsignificant.

Pairwise comparisons indicated that, in agreement with previous data (Miller, Jagielo, & Spear, 1989, 1990, 1991), the subjects given no prior-cuing treatment and conditioned with either the CS−/CS+ or CS+/CS− procedures did not differ from their respective unpaired control group in time spent in the CS+. This indicates that conditioning is not expressed at a 3-h retention interval in the absence of a prior-cuing treatment and that retention is not enhanced by reversing the usual order of stimulus presentation during conditioning.

Prior-cuing effects after CS−/CS+ conditioning. The subjects conditioned with the CS−/CS+ procedure and given pretest exposure to the CS− expressed a strong aversion to the CS+ relative to unpaired control subjects, consistent with previous results (Miller, Jagielo, & Spear, 1989, 1990, 1991). Exposure to the US and to the CS− and US combined also served as effective prior-cuing treatments for the subjects in the CS−/CS+ condition. A comparison of *paired* subjects conditioned with the CS−/CS+ procedure indicated that those given the CS−, US, or CS− and US combined spent significantly less time in the CS+ than did subjects not given prior cuing. This provided further confirmation that these stimuli served as effective reactivation treatments. Paired subjects given prior cuing with the CS− spent significantly less time in the CS+ than did subjects given prior cuing with the CS− and US combined. The difference between

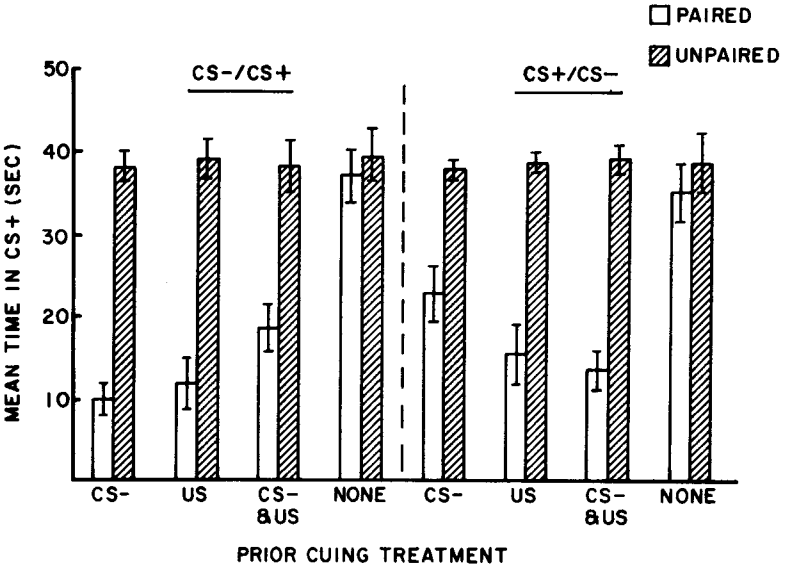

Figure 2. Mean seconds spent in CS+ by subjects conditioned with the CS−/CS+ or CS+/CS− procedure and given various prior-cuing treatments. (Vertical lines indicate standard errors of the mean.)

paired subjects given pretest exposure to the US and those given prior cuing with the CS− and US combined approached but did not reach statistical significance (mean difference = 7.16; critical value needed for statistical significance = 7.78).

Prior-cuing effects after CS+/CS− conditioning. The three prior-cuing treatments also resulted in the expression of a conditioned aversion for the subjects conditioned with the CS+/ CS− procedure; the subjects in all of these prior-cuing treatment conditions spent significantly less time in the CS+ than did subjects in the respective unpaired control conditions. A comparison of paired subjects conditioned with the CS+/CS− procedure and given the various prior-cuing treatments indicated that the subjects given pretest exposure to either the CS−, US, or CS− and US combined spent significantly less time in the CS+ than did subjects not given prior cuing, providing further confirmation that these stimuli served as effective reactivation treatments.

In contrast to the results obtained when the subjects were given CS− exposure prior to the CS+ during conditioning, the CS− appeared to serve as a less effective cue for the reactivation of the target memory than did pretest exposure to the other two prior-cuing treatments. The subjects given pretest exposure to the CS− and US combined spent significantly less time in the CS+ than did subjects given prior cuing with the CS− alone. The trend for the subjects given pretest exposure to the US to spend less time in the CS+ than subjects given prior cuing with the CS− alone approached, but did not reach, statistical significance (mean difference = 7.42; critical value needed for statistical significance = 7.78).

Further evidence for the differential effectiveness of the CS− as a reactivation treatment is provided by a *direct* comparison of paired subjects given prior cuing with the CS− in the two stimulus-order conditions during training. The subjects conditioned with the CS−/CS+ procedure and given prior cuing with the CS− spent significantly less time in the CS+ than did the subjects trained with the CS+/CS− procedure and given prior cuing with the CS−. A similar comparison across the two stimulus-presentation conditions indicated that there was no significant difference between paired subjects given prior cuing with the US. The trend for the CS− and US combined to serve as a more effective prior-cuing treatment for the subjects conditioned with the CS+/CS− procedure also did not reach statistical significance. Finally, there were no significant differences in time spent in the CS+ among the subjects in any of the unpaired control conditions.

GENERAL DISCUSSION

In Experiment 1, 18-day-old rats were given exposure to CS− either before or after the pairing of CS+ with footshock and were immediately tested for an aversion to CS+. The results indicated that the subjects in both the CS−/CS+ and CS+/CS− conditions acquired an aversion to the CS+, and the strength of this aversion was not affected by the order of stimulus presentation. This absence of an effect of stimulus-presentation order is in contrast to results we previously reported for visual conditioning with similar training procedures (Miller, Jagielo, Gisquet-Verrier, & Spear, 1989). The rats were slightly younger (16 days postnatal); but although this age difference might be significant for such conditioning, a procedural difference seems more likely to account for this discrepancy. In those studies, the subjects were exposed to a white chamber (the CS−) either prior to or following the pairing of a black chamber (the CS+) with footshock. When given a preference test between the white and black chambers, the subjects given CS− exposure prior to the CS-US pairing expressed an aversion to the black chamber, whereas subjects in the CS+/CS− condition did not. Subsequent experiments indicated that in the CS+/CS− condition, the CS− had itself become aversive because of a backward pairing of the footshock and the CS−. When these subjects were given a choice between the CS+ and the CS− in the preference test, they did not avoid the CS+ since both of the stimulus alternatives had become aversive during conditioning, so the relative preference for the two stimuli was not significantly different. In the present experiments, by testing the preference for the CS+ against a novel odor, the associative influence of the CS− on responding to the CS+ is removed from the test situation, and as a result the subjects in each of the stimulus-presentation conditions expressed comparable aversions to the CS+.

In addition to expressing comparable aversions immediately after conditioning, later retention of the conditioned aversion without prior cuing also was not different for the subjects given the two orders of stimulus presentation. Forgetting appeared to be essentially complete at 3 h after conditioning in the absence of a reactivation treatment.

The alternative prior-cuing treatments were differentially effective in resulting in the expression of the conditioned aversion at this retention interval. Furthermore, the effectiveness of a given prior-cuing treatment depended on the order of stimulus presentation used during conditioning. Pretest exposure to the US was an effective cue for reactivation of the memory for subjects in both the CS−/CS+ and CS+/CS− conditions. In our previous reports (Miller et al., 1990, 1991), the US served as an effective prior-cuing treatment. In those studies, however, the US was always presented in the same context in which the animal had been exposed to the US during conditioning. In the current report, prior cuing with the US occurred in a context where the subject had not previously been exposed to the US (the room in which the subject was exposed to the CS− during training). Given the obvious significance of this stimulus event for the animal, it is perhaps not too surprising that the effectiveness of the US as a prior-cuing treatment did not seem to be significantly affected by this stimulus change from training to the time that prior cuing occurs.

Pretest exposure to the CS− and US combined was also an effective reactivation treatment for the subjects conditioned with either order of stimulus presentation. Perhaps

the most interesting comparison is between the subjects given this prior-cuing treatment and those receiving only one of the single elements as a reactivation treatment. Within the CS−/CS+ condition, the combination of CS− and US added no prior-cuing effectiveness beyond that seen with either reactivation treatment alone. This apparently was not merely due to a "ceiling" effect on measurement, an inability to detect stronger retention; the CS− and US combined served as a somewhat weaker reactivation treatment than did the US alone and was a significantly poorer reactivation treatment than the CS− alone. It seems likely that the stimulus change resulting from presenting these elements together for the first time rendered the CS− and US combined as a less effective reactivation treatment than presenting the elements singly, as they occurred during conditioning.

Within the CS+/CS− condition, the US alone and the CS− and US combined were similarly effective as prior-cuing treatments. If stimulus change from training to the time of prior cuing accounts for the less effective reactivation of memory in the subjects conditioned with the CS−/CS+ procedure and given prior cuing with the CS− and US combined, why does this same reactivation treatment seem to be as effective as the US alone for the subjects conditioned with the CS+/CS− procedure? The greater effectiveness of this reactivation treatment for these (CS+/CS−) subjects may be due to the associative status of the CS− in this training condition. Given that, in the CS+/CS− condition, the CS− acquires aversive properties due to its contiguity with the US (Miller, Jagielo, Gisquet-Verrier, & Spear, 1989), the presentation of the CS− with the US during prior cuing would constitute less of a stimulus change from the time of such conditioning to the time of prior cuing than for rats given the CS−/CS+ order during conditioning.

Exposure to the CS− prior to testing also resulted in the expression of an aversion to the CS+. However, the effectiveness of the CS− as a reactivation treatment depended on the order in which the subjects were exposed to stimulus events during training. The CS− served as a significantly more effective reactivation treatment when the subjects were exposed to the CS− prior to the CS+ than when the subjects were given the CS-US pairing prior to CS− exposure. This differential effectiveness of the CS− as a reactivation treatment could be because of the fact that in the CS+/CS− procedure, the CS− does not predict that the CS+ will be followed by footshock, whereas when the order of stimulus presentation is reversed (CS−/CS+), the CS− reliably predicts the CS-US pairing, suggesting that the information value of the CS− is critical in determining its effectiveness as a reactivation treatment.

We must, however, consider one alternative explanation for the differential effectiveness of the CS− as a reactivation treatment. It is possible that in the CS+/CS− condition, the CS− could become aversive because of the backward pairing of the US and CS−. If this aversion to CS− then generalized to the novel test odorant (orange), this generalized aversion would appear as a greater preference for methyl (a weaker conditioned aversion to CS+) during the preference test for subjects in this (CS+/CS−) treatment condition. The observation of comparable conditioning in the subjects trained with the two orders of stimulus presentation in Experiment 1 provides no suggestion of a generalized aversion to the orange test stimulus in the CS+/CS− condition when the subjects were tested *immediately* after conditioning. However, given evidence that generalization gradients flatten over time (Riccio, Richardson, & Ebner, 1984; D. A. Thomas & Riccio, 1979; D. R. Thomas, 1981), this does not rule out the possibility of generalized backward conditioning at the longer (3-h) retention interval. An examination of the test data in Figure 2 seems inconsistent with the view that the relative preference for the CS+ at the time of testing is affected by backward conditioning to the CS− that generalizes to the test stimulus 3 h after conditioning. The influence of generalized backward conditioning is not evident in the subjects given no prior-cuing treatment. Presumably such an influence would have taken the form of an increase in preference for CS+ relative to the subjects conditioned with the CS−/CS+ procedure. However, it seems reasonable to assume that backward conditioning, like forward conditioning, simply might not be expressed at this longer retention interval, suggesting that the expression of this generalized backward conditioning would depend on the administration of a prior-cuing treatment. If backward conditioning of the CS− in the CS+/CS− condition generalized to the orange test stimulus, we would expect this to influence (increase) preference for the CS+ regardless of the particular prior-cuing treatment used. The aversion to CS+ for the subjects given prior cuing with the US is not weaker for the subjects trained with the CS+/CS− procedure relative to the subjects trained with the CS−/CS+ procedure given the same prior-cuing treatment. Evidence from other experiments (Miller et al., 1990) also suggests little generalization between lemon and orange odors for the subjects at this age when testing occurs 3 h after conditioning. In one of these studies, the subjects were trained with the current one-trial conditioning procedure and tested for conditioned aversions to the CS+ in either a preference test between the CS+ and the novel orange odorant or between the CS+ and the CS− (lemon). The results indicated that conditioning was expressed 3 h after training only if the CS− (but not the orange odorant) was also present at the time of testing. These results provide additional evidence that when animals are tested at the 3-h retention interval used in Experiment 2 they clearly discriminate between the lemon and orange odors and that one odor cannot be functionally substituted for the other. These data are uniform in suggesting that the differential effectiveness of the CS− as a reactivation treatment observed in the present experiments is not due to backward conditioning of the CS− that generalized to the orange test stimulus. Rather, the collective data suggest that the greater effectiveness of the CS− as a reactivation treat-

ment in the CS−/CS+ condition is related to its ability to signal the CS-US pairing. Successful reactivation of memory may, in part, depend on the information that the reactivation treatment provides to the subject regarding the relationships among other stimuli present during the conditioning episode.

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