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Pavlovian Conditioning: The CS-UR Relation

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A new Pavlovian procedure used fluid-elicited throat-movement responses of the pigeon (N = 66) to study the effects on conditioning of the temporal relation of the CS to the US/UR. Because the throat-movement response has a substantial latency and duration, the relation of the CS to the US and UR could be independently evaluated. Four experiments indicated that, operationally, the relation of the CS to the UR—not the US—is critical for conditioning in this preparation. The conventional emphasis upon CS-US relations is based upon procedures that confound the occurrence of the US with the UR and that foster generalization decrement between training and testing. We indicate how several conditioning phenomena may be reinterpreted in terms of CS-UR relations.

The purpose of these experiments was to re-examine the nature of the events that are critical for Pavlovian conditioning. In the Pavlovian procedure, a "neutral" stimulus (the conditioned stimulus or CS) is presented prior to an eliciting stimulus (the unconditioned stimulus, or US) that evokes a response (the unconditioned response, or UR). Because the experimenter manipulates the relation between stimuli—the CS and US—these events have conventionally been assigned primary importance in theoretical interpretations of Pavlovian conditioning (cf. Rescorla, 1991). However, typical experimental preparations often employ short-latency, brief-duration URs (such as the nictitating-membrane response of the rabbit; e.g., Gormezano, Kehoe, & Marshall, 1983) or URs that are not directly measured (such as conditioned suppression; e.g., Estes & Skinner, 1941). In these preparations the effect of the CS-US relation cannot be experimentally separated from the CS-UR relation because the occurrence of the US and UR are confounded in the first instance and indeterminate in the second. In recognition of this state of affairs, some have taken care to describe the Pavlovian procedure as one that manipulates the CS-US/UR relation, not merely the CS-US relation (Gormezano & Kehoe, 1981). The typical Pavlovian procedure also evaluates conditioned responses (CRs) during periods when the CS is presented alone. Presenting the CS when the US is absent avoids the intrusion of URs into the time period in which CRs are measured. However, this test procedure inherently favors responding after training with a forward CS-US/UR relation because the CS has previously occurred alone only after training with a forward relation. That is, generalization decrement from training to testing is minimized when a CS-alone test procedure is employed in conjunction with a forward CS-US/UR procedure. Rescorla (1981) has recognized this potential source of bias and demonstrated its effects in a series of experiments using compound conditioned stimuli.

To investigate the effects on conditioning of CS-US and CS-UR relations and the contributions of generalization decrement to the assessment of conditioned responding, we developed a Pavlovian preparation in which the UR has an appreciable latency and duration. With a UR of longer latency, the ordinal temporal relation of the CS to the UR can be made to differ from that of the CS to the US. This is accomplished by introducing the CS after US onset but before UR onset. If a long latency UR also has a substantial duration, procedures can be implemented that eliminate a forward temporal relation of the CS to either the US or the UR, but maintain overlap between the CS and UR. This is accomplished by introducing the CS after the onset of the UR or by extending the CS after the onset of the UR. Through these procedures, the contribution to the conditioning process of CS-US and CS-UR relations and of CS-UR overlap (i.e., CS-UR temporal contiguity) can be examined.

In Experiment 1, a conditioning preparation was developed that used the restrained pigeon as the subject and water-elicited throat-movement responses (TMRs) as the UR. Given the outcome of Experiment 1, a series of experiments were conducted that instituted various temporal relations between the CS and the long-latency, temporally extended TMR. Experiment 2 studied the effects of a backward CS-US relation with a forward CS-UR relation (hereafter, a US-CS-UR procedure) and of a backward relation of the CS to both the US and UR (hereafter, a US-UR-CS procedure). If conditioning occurs with a US-CS-UR procedure, then a forward CS-US temporal relation is not required for conditioning. If conditioning occurs with a US-UR-CS procedure, then CS-UR overlap is sufficient for conditioning and a forward temporal relation of the CS to either the US or the UR is not required. It should be emphasized that the occurrence of conditioned responding with these special procedures does not deny that a forward CS-US relation may affect the level of responding through minimizing generalization decrement from training to testing or that temporal relations among stimulus components of multi-element CSs may also affect responding (e.g., Holland, 1990a, 1990b; Kehoe, Horne, Macrae, & Horne, 1993; Kehoe, 1982; Kehoe & Napier, 1991; see also Holland, 1977). In Experiment 3, we studied the effects of a forward CS-US/UR procedure and manipulated CS-UR overlap by extending the CS past the onset of the UR (hereafter designated extended CS procedures). Extended CS procedures permit the effects of CS-UR contiguity to be studied with generalization decrement reduced because the CS occurs alone during both training and testing. Experiment 4 also employed an extended CS procedure, but used a different US to clarify the interpretation of Experiment 3. Presentation of the experiments emphasizes the operationally defined relations between CS, US, and UR. Consideration of more general experimental and theoretical implications of the research is largely postponed until the General Discussion.

Experiment 1

To meet the experimental requirements, we developed a Pavlovian conditioning preparation that used the pigeon as the subject and the injection of water into the oral cavity as the US. The resulting bout of TMRs served as the UR (Vegas, 1995). Prior work has shown that the pigeon adapts well to restraint during Pavlovian conditioning (cf. Stickney, Donahoe, & Carlson, 1981) and that nictitating membrane conditioning in the pigeon is comparable to that of the rabbit (Burns, 1989; Schwartz, 1988). In addition, other research has demonstrated that mandible movements of the pigeon are conditionable using the opportunity to drink as the US (Remy & Zeigler, 1993; cf. Woodruff & Williams, 1976). Finally, the pigeon has been extensively studied as a subject in the Pavlovian procedure of autoshaping (e.g., Brown & Jenkins, 1968; Rescorla, 1977) and in a wide variety of operant procedures (e.g., Ferster & Skinner, 1957; Honig & Staddon, 1977).

To demonstrate conditioning, we gave two experimental groups of pigeons forward CS-US pairings at interstimulus intervals (ISIs) of either 1,000 or 1,500 ms. A control group was exposed to explicitly unpaired presentations of the 1,000-ms CS and the US. To further characterize the unconditioned TMR, US-alone presentations were administered at the conclusion of conditioning.

Method

Subjects. Sixteen experimentally naïve White Carneaux pigeons (Columba livia) of undetermined sex, derived from stock obtained from the Palmetto Pigeon Plant (Sumter, SC), served as subjects. Their ages ranged from 2 to 6 years.

Apparatus. The experiment was conducted in two sound-attenuating, electrically shielded chambers (74 cm x 59 cm x 61 cm). Each chamber was ventilated by a fan, continuously illuminated by a 15-W houselight, and provided with a white noise (80 dB re 0.0002 dynes/cm^2) that served as a masking stimulus. The subjects were restrained by an apparatus similar to that previously used in conditioning the pigeon NMR (Stickney et al, 1981). The bird's body was confined in a canvas jacket held in place by Velcro straps and suspended from a horizontal rod attached to a ring stand. The neck was placed in a slot on a horizontal neck holder to which were attached the mandible and head restraints. (See Figure 1.) The mandible restraint limited lateral movements of the beak, while permitting dorso-ventral movements of the upper and lower mandibles. The head restraint—in concert with the neck holder—minimized lateral, dorsal, and posterior head movements. Felt pads (not shown in Figure 1) were affixed to all surfaces of the restraining device that came into contact with the head to hold it comfortably in place. When head movements had been restrained, a 3-mm thick bit was placed between the mandibles. The bit extended approximately 3 mm into the oral cavity and contained in its center a blunted cannula needle (2.5-mm outside diameter) whose tip co-terminated with the end of the bit. The water US was injected into the back of the oral cavity via a gravity-fed system from a reservoir located above the chambers. Electrically operated valves controlled the duration (volume) of the US. The CS was a 1.8-cm circular visual stimulus placed 1 cm in front of the left eye, subtending a visual angle of approximately 80 degrees. The CS was produced by passing white light from two 6 VDC bulbs (No. 44) through a No. 73 Wratten filter whose peak transmission was 576 nm (appearing green to a human observer) and a No. 2E Wratten filter that excluded wavelengths below 415 nm (ultraviolet) to which pigeons are sensitive (Wright, 1972).

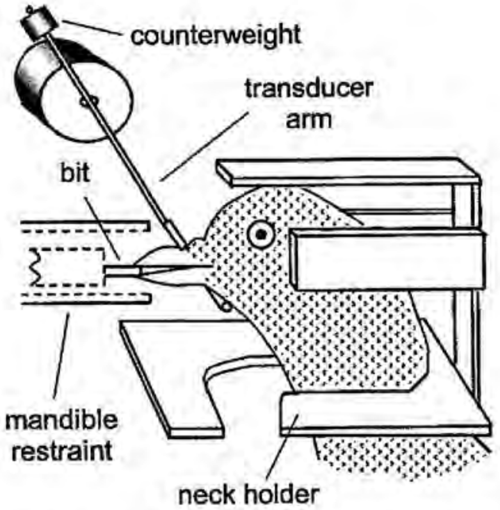

Figure 1. Schematic drawing of the apparatus that immobilized the pigeon's head, injected fluid into the oral cavity, and monitored throat movements.

Water-elicited TMRs served as the UR. TMRs were monitored by a transducer arm held against the throat of the pigeon by a counterweight. The transducer arm was positioned at the point of maximum displacement of the throat during swallowing (approximately 50 mm posterior to the junction of the lower mandible with the feathered throat). Movement of the throat caused the arm to rotate a polarizing filter that varied the intensity of light from a photodiode falling on a phototransistor located within the transducer housing (Gormezano & Gibbs, 1988). The varying output voltage of the phototransistor was sampled by a Data Translation 2808, 10-bit, analog-to-digital (A/D) converter at a 2-ms rate during 3-s trial periods when stimuli were presented and at a 50-ms rate during intertrial intervals (ITIs). A computer located in an adjacent room recorded the data on its hard drive and implemented the various conditions.

Procedure. Birds were reduced to 85% of their free-feeding weight and then, 8 days prior to the beginning of the experiment, placed on a 22-hr water-deprivation schedule with free access to water during the remaining 2 hrs. Pilot work indicated that pigeons ingest essentially their full daily intake of water within a 2-hr period after feeding (Vegas, 1995). During the experiment, birds were fed one tablespoon of pigeon chow (approximately 9 g) 30 min prior to each session. This regimen promoted avid drinking during the experimental session. Thirty minutes following the experimental session, birds were given 2-hr access to water and a supplementary food ration that was adequate to maintain 85% body weight. Experimental sessions were conducted 5 to 7 days per week and the deprivation schedule was continuously maintained.

Each bird was first individually adapted to the test chamber during two 30-min daily sessions. The stimulus-producing and TMR-monitoring devices were positioned as during experimental sessions, but no stimuli were presented although TMRs were recorded.

Eight subjects were randomly assigned to either of two experimental groups given forward CS-US/UR trials with either a 1,000-ms CS ($\underline{n}$ = 4) or 1,500-ms CS ($\underline{n}$ = 4). Eight additional control subjects were given either explicitly unpaired trials ($\underline{n}$ = 4) or US-alone trials ($\underline{n}$ =4). The initial characterization of the UR was based upon US-alone observations from the eight control subjects. The final characterization of the UR included observations from these subjects supplemented by observations from 28 additional birds that were given US-alone presentations after the completion of various treatments described in Experiment 3 (Vegas, 1995).

For the four birds that received only US presentations, each session consisted of 10 US-alone trials. The ITI was a variable 2 min with a minimum of 1 min between trial periods. Three US durations (volumes) were used—100 ms (0.25 ml), 150 ms (0.45 ml), and 200 ms (0.65 ml)—with each animal receiving 4½ US-alone sessions at each value. The differing US durations were used to determine the US magnitude at which TMRs were reliably elicited. All subjects in the US-alone group were first exposed to the 100 ms US. Then the two longer US durations were presented in counterbalanced order with two birds exposed first to the 150-ms US and two to the 200-ms US.

The two experimental groups that received forward CS-US/UR presentations were conditioned with either a 1,000-ms or a 1,500-ms ISI. In both groups, the CS was extended for 200 ms past US onset, which allowed the CS to overlap the 200-ms US. Thus, the total duration of the CS was either 1,200 or 1,700 ms. Each conditioning session consisted of 30 trials—28 paired CS-US trials and 2 CS-alone probe trials presented on trials 11 and 26. A total of 10 conditioning sessions was given. The explicitly unpaired control group received the same number of presentations of the 1,200-ms CS and the 200-ms US as its companion paired group with an average ITI of 1 min and a 30-s minimum ITI. In this way, the average time between USs was the same for the experimental and the explicitly unpaired control groups. At the conclusion of the experiment, subjects in the two experimental and the explicitly unpaired control groups were given a half session of five US-alone presentations to further characterize the latency and duration of the UR.

The reliability of findings was assessed using analysis-of-variance methods followed by planned comparisons to evaluate the experimental hypotheses. The alpha level for the F tests was .05 for all comparisons in this and subsequent experiments.

Results and Discussion

We first characterize the TMR as a UR and then describe conditioning of the TMR.

Characterization of the UR. The latency distributions of URs produced by the three US durations in the US-alone group indicated that the 200-ms US elicited URs most reliably; i.e., on more than 95% of the presentations. The modal latency of the UR was greater than 250 ms for all US magnitudes, but the variability of the latencies decreased as the magnitude increased. The latencies of all URs evoked by a 200-ms US in the US-alone group, in the explicitly unpaired control group, and on US-alone trials following various conditioning treatments in this experiment and Experiment 3 were combined to produce the distribution of UR latencies shown in Figure 2. Combining the latency distributions was warranted because the median latencies obtained after the various treatments did not differ appreciably or systematically: In the preliminary study of US magnitude the median latency of a TMR was 364 ms after exposure to only the US, in the explicitly unpaired control group it was 394 ms after exposure to both the CS and US, and in Experiment 3 it was 364 ms after extensive CS-US pairings (see Vegas, 1995). Thus, the latency of the UR in this preparation was essentially unchanged by the number of US presentations (cf. Schreurs, Shi, Pineda, & Buck, 2000).

The following criteria were used for scoring URs: (a) No TMR was scored if it was preceded on that trial by a TMR that began in the 100-ms interval before the US was presented. This minimized distortion of the UR latency distribution by inclusion of “spontaneous” TMRs. (b) All criterion TMRs had a maximum amplitude that differed from the mean baseline position during the preceding ITI by more than 2.33 standard deviations (SDs). (A TMR with a standard score greater than 2.33 z occurs by chance with $p < .01$ given a normal distribution of intertrial TMR amplitudes.) The SD measured variation in the throat position during the ITI, with the initial 20 s of all ITIs excluded from the calculation to minimize any persisting effects of stimuli from the preceding trial period. The amplitude of a TMR was expressed as a z score so that small day-to-day variations in the placement of the transducer arm on the throat of the pigeon would have little effect on the response criterion. The obtained median SD of intertrial TMRs was 0.14 mm and the obtained median amplitude of URs was 4 z (i.e., 5.4 mm). (c) Criterion TMRs had to exceed a minimum duration of 10 ms, with the beginning of a response defined as a deviation of 0.05 mm from the mean baseline throat position during the preceding ITI and the termination of a response defined as a return to within 0.05 mm of the baseline position or a fall of more than 80% from the peak TMR amplitude before a change in the direction of a TMR of at least 0.5 z indicated that onset of a possible subsequent response had been detected. These scoring criteria were implemented by a computer program. The obtained median duration of individual TMRs was 100 ms, which falls within the range reported for the duration of jaw movements elicited by water in the pigeon (Remy & Zeigler, 1993). Close visual observation of the pigeon when TMRs were detected indicated that TMRs reflected swallowing as well as shorter duration tongue movements that are components of the swallowing reflex (cf. Zweers, 1982; Klein, LaMon, & Zeigler, 1983). The duration of a bout of TMRS ranged from 2 to 5 s measured from the onset of the first TMR to the termination of the last TMR of the bout. The obtained distribution of UR latencies indicated that a 200-ms US elicited a bout of URs whose median latency was 282 ms.

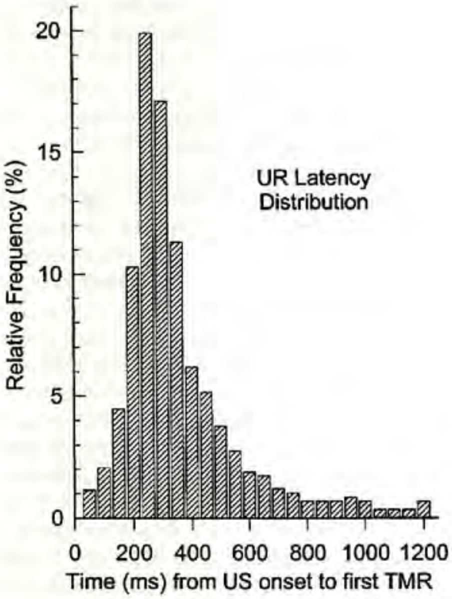

Figure 2. Relative frequency distribution of the latencies of bouts of throat-movement responses (TMRs) elicited by a 200-ms jet of water into the oral cavity of the pigeon. The distribution is based on observations of 1,401 bouts of TMRs. US = unconditioned stimulus; UR = unconditioned response.

Conditioning of the TMR. Performance during conditioning sessions was assessed by two measures—the percentage of CS presentations with at least one TMR and the rate of TMRs. To qualify as a CR, TMRs had to satisfy the same response criteria as URs and, in addition, to occur between 50 ms after the onset of the CS and 150 ms following the onset of the US (i.e., before URs were elicited). A second measure—the rate of TMRs during the CS—was possible because the US elicited a bout of URs instead of a single UR as in many conditioning preparations.

Figure 3 depicts the percentage and rate measures for the 1,000-ms and 1,500-ms ISI experimental groups that received CS-US/UR pairings and for the explicitly unpaired control group. The leftmost set of points in Figure 3 shows mean responding during the two pre-experimental adaptation sessions before the CS and US were presented; i.e., during contextual stimuli (Ctx) alone. Responding during Ctx was measured for time periods of the same length as the CSs that occurred in subsequent sessions. The percentages of TMRs (upper panel) and rates of TMRs (lower panel) during Ctx were low, indicating a suitable baseline from which to detect increases in responding. The low baseline levels prior to conditioning were representative of subsequent experiments and are not reported hereafter.

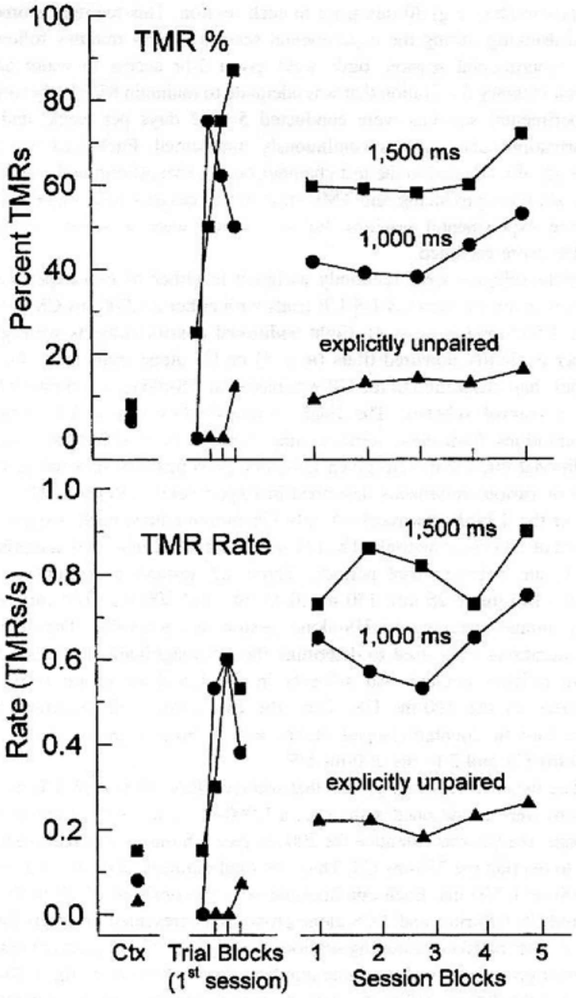

Figure 3. Conditioning of the throat-movement response (TMR). Performance is shown for independent groups in which the conditioned stimulus (CS) and unconditioned stimulus (US) were paired with a 1,000-ms interstimulus interval (ISI) or with a 1,500-ms ISI and in which the CS and US were explicitly unpaired. Responding during comparably long periods in adaptation sessions when only stimuli from the experimental context (Ctx) were present is shown by unconnected symbols in the leftmost portion of the figure. Responding during the first seven CS presentations of the first session are shown in the middle portion of the figure for the first trial separately and for the next six trials in two-trial blocks. Responding during the 10 sessions in which the CS and US were presented is shown in the rightmost portion of the figure in two-session blocks. The upper panel shows the mean percentage of trials with at least one TMR; the lower panel shows the mean rate of TMRs.

Acquisition of the TMR is shown in the central portion of Figure 3 during the first seven trials in which the CS was presented. Responding is shown separately for the first CS presentation and, thereafter, for blocks of two trials during the next six trials. Responding in the first CS presentation did not differ from the Ctx baseline; that is, so-called alpha responses were not elicited by the CS. Once CS-US pairings began, responding rapidly increased in both paired groups. Records of individual subjects in the paired groups indicated that the first CR occurred during the third trial on the average. Prior work has shown that conditioning proceeds very rapidly when a liquid US is injected directly into the oral cavity (e.g., Trowill, Panksepp, & Gandelman, 1969; cf. Gormezano et al, 1983). Responding in the explicitly unpaired control group remained at low levels throughout the first seven CS presentations.

Performance during all ten sessions in which the CS and US were presented is shown in the rightmost portions of Figure 3 in blocks of two sessions. Responding during the CS was elevated for both of the groups that received CS-US pairings and to a lesser extent for the explicitly unpaired group. This pattern of findings was obtained whether measured by the percentage of CSs with at least one TMR (upper panel) or the rate of TMRs during the CS (lower panel). Statistical tests supported these conclusions. Because the level of responding did not vary systematically over sessions, comparisons were based on the mean responding over all conditioning sessions. The percentage of trials with a TMR and the rate of TMRs were both reliably greater during experimental sessions than adaptation sessions for the 1,000-ISI group, Fs (1, 3) = 87.2 and 99.4, respectively, and for the 1,500-ISI group, Fs (1, 3) = 80.3 and 28.4, respectively. Finally, responding during the CS was greater in the 1,500-ms paired group than the 1,000-ms group as measured by both the percentage and rate of responding; Fs (1, 9) = 13.35 and 5.35, respectively.

For the explicitly unpaired control group, the percentage of trials with a TMR and the rate of TMRs were also reliably higher during experimental sessions than adaptation sessions, Fs (1, 3) = 52.9 and 17.1, respectively. However, the level of responding during the CS was greater for the CS-US paired groups as a set than for the explicitly unpaired control group when measured by either the percentage of trials with a TMR or the rate of TMRs; Fs (1, 9) = 70.16 and 13.74, respectively. The increase in responding during the CS in the explicitly unpaired control group did not reflect an indiscriminate increase due to the conjunction of the US with contextual stimuli: The variability of throat movements for the unpaired group, as measured by the standard deviation of TMRs during the ITI, did not increase from the value during adaptation sessions ($F < 1$) and did not differ from that of the two paired groups; F (1, 11) = 1.48, $p > .25$. Thus, responding during CS in the explicitly unpaired group most likely reflects pseudoconditioning (cf. Sheafor, 1975).

In summary, Experiment 1 demonstrated that conditioning occurred with a forward CS-US/UR procedure. Responding during the CS increased somewhat whether the CS was paired or unpaired with the US, but the increase was much greater for the paired CS. The absolute level of conditioned TMRs was moderate (approximately 65% of the CS trials contained a CR with a 1,500-ms ISI). This level of responding is lower than the level of more than 90% obtained with the short-latency, brief-duration NMR of either the pigeon (e.g., Burns, 1989) or rabbit (e.g., Gormezano & Kehoe, 1981). It is of interest that the level of responding observed with the TMR parallels previous findings with another long-latency, long-duration response—the jaw-movement response (JMR) of the rabbit evoked by the injection of water into the oral cavity (e.g., Mitchell & Gormezano, 1970; Sheafor, 1975; Sheafor & Gormezano, 1972; Smith, DiLollo, & Gormezano, 1966). A possible origin of the difference between long- and short-duration URs may be that, in the former case, the UR persists during the contextual stimuli that follow the offset of the CS. If contiguity of the UR with Ctx promotes conditioning to Ctx, then a greater opportunity for contextual conditioning would occur with long duration URs. Greater contextual conditioning could affect the level of responding to the CS through either or both of the following: (a) sensitization or disinhibition by the unpaired CS of responses conditioned to Ctx (e.g., Harris, 1941; Pavlov, 1928, p. 381; Servatius & Shors, 1994) or (b) partial blocking of conditioning to the paired CS by context conditioning (e.g., Randich & LoLordo, 1979). We return to the role of context conditioning in Experiment 3.

Experiment 2

Experiment 1 indicated that the long-latency, long-duration TMR provides a means to distinguish between the contributions of CS-US and CS-UR temporal relations to Pavlovian conditioning. To assess their contributions, we instituted three procedures in Experiment 2. In the first procedure, the US-CS-UR procedure, the CS precedes and overlaps the UR, but follows US onset. (Note, this procedure is a backward CS-US procedure. The latter terminology is not used here because it does not distinguish procedures in which the CS follows both the US and UR from those in which the CS follows only the US.) If conditioning occurs with a US-CS-UR procedure, then a forward CS-US temporal relation is not required for conditioning.

Two caveats are in order when assessing conditioning during training procedures in which the CS follows the US on paired trials: First, responding cannot be measured during paired trials because CRs are co-mingled with URs. Responding can only be measured on probe trials in which—by definition—the CS is presented alone. Second, and more fundamentally, on probe trials the CS cannot be presented in the full stimulus context in which it appeared on paired trials. With a US-CS-UR procedure, the CS on paired trials occurs in the context of the US and—during the later portion of the CS—perhaps stimuli produced by the UR as well. If sensory consequences of the US are components of the stimulus complex that acquires control over responding during acquisition, the level of CRs on CS-alone probe trials would be reduced; i.e., generalization decrement would occur. Generalization decrement is inevitable when conditioning is assessed during the CS after other than forward CS-US/UR procedures (cf. Miller & Barnet, 1993; Rescorla, 1981).

The second procedure implemented in Experiment 2 was a US-UR-CS procedure in which the CS is presented after the onsets of both the US and the UR, but overlaps the extended UR. If conditioning occurs with a US-UR-CS procedure, then CS-UR overlap is sufficient for conditioning and neither a forward CS-US nor a forward CS-UR temporal relation is necessary. However, generalization decrement on probe trials with the US-UR-CS procedure is potentially even more likely: CS onset occurs after both US onset and any sensory feedback from the UR. To reduce generalization decrement for both the US-CS-UR and US-UR-CS procedures, we instituted an additional type of probe trial, termed an augmented probe trial, after conditioning was first assessed using regular CS probe trials in which the CS was presented alone. On augmented probe trials, a drop of water was administered prior to the CS at the time that US onset occurred on paired trials. Augmented probe trials reinstated some of the sensory consequences of the US and, thereby, more nearly reproduced the full stimulus context in which the CS appeared on paired trials. (Findings to be reported later indicate that the drop of water did not, by itself, evoke TMRs and, hence, any sensory feedback from the UR was not reinstated.)

Conditioning with a backward CS-US/UR relation has been found in other preparations, although not invariably (for reviews, see Cautela, 1987; Hall, 1984; Spetch, Wilkie, & Pinel, 1981). Of greatest relevance to the present research is the effect of the duration of the UR on backward conditioning. In preparations in which the US evokes short-duration URs, such as air-puff-elicited NMRs, conditioning has generally not been found with a backward CS-US relation (e.g., Aou, Woody, & Birt, 1992; McNish, Betts, Brandon, & Wagner, 1997; Plotkin & Oakley, 1975; Siegel & Domjan, 1971, 1974; Stern & Frey, 1978). In contrast, preparations employing USs that evoke long-duration URs have more often promoted conditioning, such as poison-elicited nausea (e.g., Yamamoto, Shimura, Sako, Yashoshima, & Sakai, 1994; Logue, 1979;

Franchina & Deitz, 1981) or water-elicited JMRs (Tait, Quensel, & ten Have, 1987). Similarly, USs that may reasonably be assumed to evoke long-duration—albeit unmeasured—URs, such as the autonomic responses elicited by shock in conditioned-suppression and conditioned-punishment procedures, have also often produced conditioning with backward CS-US arrangements (e.g., Albert & Ayres, 1997; Ayres, Haddad, & Albert, 1987; Bevins & Ayres, 1992; Heth & Rescorla, 1973; Keith-Lucas & Guttman, 1975; Overmeir & Murison, 1993; Tait & Saladin, 1986; Van Willigen, Emmett, Cote, & Ayres, 1987).

The third procedure in Experiment 2 was a forward CS-US/UR procedure that replicated the stimulus arrangements of Experiment 1, but with a small change: The CS was presented prior to the US but, unlike Experiment 1, terminated before US onset (hereafter, this procedure is designated the CS - - US-UR procedure). The earlier termination of the CS prevented overlap of the CS with either the US or UR while ensuring that the CS preceded both events. Of course, any behavioral or neural processes that were initiated by the CS and that persisted until US and UR onset could overlap the US/UR. The CS—US-UR procedure in Experiment 2 may also be described as a trace CS-UR procedure in which the duration of the trace interval is equal to the latency of the UR. Because it is well established that conditioning occurs with such a temporal arrangement in other preparations (e.g., Pavlov, 1927; Schneiderman, 1966), the CS - - US-UR procedure provides further evidence of the conditionability of TMRs.

Method

Subjects. Sixteen experimentally naive pigeons of the same description as Experiment 1 served as subjects. They were maintained on an 85% food-deprivation and 22-hr water-deprivation schedule as before.

Apparatus. During experimental sessions, the pigeons were placed in the restraint apparatus, and water was again delivered from a cannula located within a bit placed between the upper and lower mandibles. In Experiment 2, two visual CSs were used—the green stimulus used in Experiment 1 and a second stimulus of the same dimensions but appearing red to a human observer. The second stimulus was produced by passing white light through a No. 819 Edmund Scientific filter and an ultraviolet filter of the same type used with the green stimulus.

Procedure. The birds were first adapted to the test chambers during two 30-min sessions. The stimulus-producing and TMR-monitoring devices were positioned in the same manner as in conditioning sessions, but no stimuli were presented.

Animals were randomly assigned to one of four groups of four subjects each. For all groups, a differential conditioning procedure was used in which one color (CS+) was paired with the US and the other color (CS-) was explicitly unpaired. CS- provided a control for any TMRs that might occur during a phasic stimulus that was not paired with the US.

In the US-CS-UR procedure, the 200-ms US was followed by the onset of a 850-ms CS+ with direct measurements[1] indicating that CS onset occurred 37 ms after US onset. With this arrangement, CS+ preceded the onset of over 90% of the bouts of TMRs elicited by the US. (All values for the temporal relation between the CS and UR were based upon the latency distribution of URs; see Figure 2.) The US-CS-UR procedure instituted a forward CS-UR relation, but a backward CS-US relation. The US-CS-UR procedure was implemented for two groups. For one group, the green stimulus served as CS+; for the other, the red stimulus served as CS+. This counterbalanced the assignment of wavelengths to the CSs for the US-CS-UR procedure.

A US-UR-CS procedure was instituted for a third group of four subjects. The 200-ms US was followed by the onset of a 850-ms CS+ after a directly measured interval of 637 ms. Based on the latency distribution of URs, the onset of CS+ occurred after over 90% of the URs had begun, thereby ensuring a backward CS-UR relation on the great majority of paired trials. In the US-UR-CS procedure, the green stimulus served as CS+ and the red stimulus as CS-. A CS—US-UR procedure was instituted for the final group, which received a 500-ms CS+ followed by a 200-ms US. Based on direct measurements of the offset of CS+ and the onset of US, CS+ overlapped only the initial 13 ms of the US and terminated before the beginning of all URs. The green stimulus served as CS+ and the red stimulus as CS-.

The experiment was carried out with two sets of 8 animals each. The first set included the CS—US-UR procedure and the US-CS-UR procedure in which the green stimulus served as CS+. The second set included the US-CS-UR procedure with the red stimulus as CS+ and the US-UR-CS procedure with the green stimulus as CS+. As noted, a differential conditioning procedure was instituted for all groups. Each conditioning session consisted of 28 trial periods with 10 paired CS+ trials, 2 CS+ probe trials (trials 6 and 20) during which CS+ was presented alone, 12 CS- trials, and 4 Ctx-alone trials during which no phasic stimulus was presented. CS+ and CS- trials were presented in pseudo-random orders in which the first-order conditional probabilities were approximately equal and no stimulus occurred more than three times consecutively. A total of 10½ conditioning sessions was given to each subject. TMRs on probe trials were scored as CRs if they met the scoring criteria described in Experiment 1 and they began between 50 ms after CS onset and the offset of the CS. The subjects trained with the US-CS-UR and US-UR-CS procedures were then given an additional 10½ sessions in which the same training regimen was followed except that CS+ probe trials were preceded by a 50-ms drop of water whose onset coincided with the time at which the 200-ms US appeared on paired trials. Following conditioning sessions, all subjects in the US-CS-UR and US-UR-CS groups were given 6 sessions with two unsignaled 50-ms water presentations interspersed among ten unsignaled 200-ms US presentations. This ensured that the subjects received the same number and duration of water presentations as had occurred during conditioning sessions to assess any responding evoked by the 50-ms water stimulus. As in Experiment 1, stimulus presentations occurred during 3-s trial periods when the A/D converter monitored TMRs at a 2-ms rate. The mean ITI was 120 s, with a minimum value of 60 s during conditioning sessions and post-experimental sessions of unsignaled water presentations. During the ITI, TMRs were monitored at a 50-ms rate.

The reliability of findings was assessed using analysis-of-variance techniques followed by planned comparisons using error terms appropriate for the effects being compared (Winer, 1971).

Results and Discussion

The findings for each of the three procedures—CS - - US-UR, US-CS-UR, and US-UR-CS—are considered in turn. Performance was measured by both the percentage of trials with at least one TMR and the rate of TMRs.

CS—US-UR procedure. The CS - - US-UR procedure provided additional evidence of the conditionability of TMRs. Because conditioning in the other two procedures could be measured only on probe trials, responding in the CS - - US-UR procedure was also assessed only on probe trials. As shown in the leftmost set of three bars in the upper and lower panels of Figure 4, conditioning occurred with a CS - - US-UR relation as measured by both the percentage of trials with a CR (upper panel) and the rate of responding (lower panel). For both dependent measures, conditioning was assessed by the difference in responding between CS+ and CS- trials. The difference measure controls for variation between procedures in responding to any phasic stimulus and in the baseline level of responding. This control was necessary because responding was particularly elevated during CS- and Ctx trial periods in the US-UR-CS procedure relative to the CS - - US-UR procedure. In only the US-UR-CS procedure, the US and the UR were not preceded by a discrete stimulus, thereby increasing the opportunity for conditioning to Ctx. Statistical analyses of the CS - - US-UR procedure indicated that the percentage of trials with a TMR and the rate of TMRs were both reliably greater during CS+ probe trials than CS- trials, Fs (1, 24) = 5.66 and 8.90, respectively. The absolute levels of responding during CS- and Ctx trials were low and similar. The differences were statistically unreliable as measured by both the percentage and rate measures; Fs < 1.

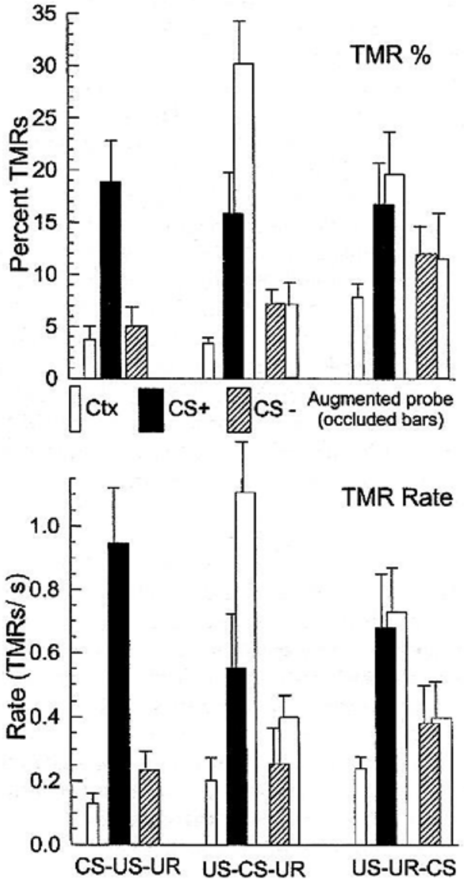

Figure 4. Effect of various CS-US-UR relations on conditioning. The leftmost sets of bars show performance for the group in which CS+ preceded both the US and UR (CS—US-UR). The middle sets of bars show performance for the group in which CS+ followed the US but preceded the UR (US-CS-UR). The rightmost sets of bars show performance for the group in which CS+ followed both the US and the onset of the UR but overlapped the UR (US-UR-CS). The leftmost unfilled bars of each set show responding during the context (Ctx) alone. Filled bars in each set show responding during CS+ (solid) and CS– (oblique lines) during probe trials. Unfilled partially occluded bars in the US-CS-UR and US-UR-CS groups show performance during CS+ or CS– when the same subjects were later tested with augmented probe trials. Error bars indicate the standard error of the means. The upper panel shows the percentage of trials with at least one throat-movement response (TMR); the lower panel shows the rate of TMRs. CS = conditioned stimulus; US = unconditioned stimulus; UR = unconditioned response; CS+ = CS paired with the US; CS– = CS explicitly unpaired with the US.

Findings from the CS - - US-UR procedure demonstrated that overlap between CS+ and the UR was not necessary for conditioning; i.e., trace conditioning occurred. This is not to say that contiguity played no role; any persisting behavioral and neural processes initiated by CS+ could overlap the US/UR. Consistent with this interpretation, the rate of TMRs was greater during the remaining portion of the 3-s probe-trial period that followed CS+ than during the comparable portion that followed CS-. The mean rates of TMRs in the post-CS portion of the trial period on CS+, CS-, and Ctx probe trials were 0.67/s, 0.16/s, and 0.08/s, respectively. Statistical analysis indicated that the TMR rate during the post-CS period on CS+ probe trials was reliably greater than following CS- trials; $\underline{F}$ (1, 6) = 12.84. The corresponding difference in TMR rates on CS- and Ctx trials was unreliable; $\underline{F} < 1$. Thus, responding was significantly elevated in the portion of post-CS+ probe trials that was contiguous with the UR on paired trials.

US-CS-UR procedure. Consider now findings from the US-CS-UR procedure in which CS+ followed the US, but preceded the UR. First, the wavelength assignments of CS+ and CS- had no effect on either measure of performance for the two groups in which wavelength was counterbalanced, $\underline{F}$s < 1. Accordingly, the results from the counterbalanced groups were combined. The middle sets of bars in Figure 4 show performance during the US-CS-UR procedure for the percentage measure (upper panel) and the rate measure (lower panel). The percentages and rates for CS+ and CS- trials are shown for regular probe trials (filled bars) and for augmented probe trials (unfilled, partially occluded bars). The percentages and rates during Ctx-alone trials are also given (the leftmost bars of the middle sets). During regular probe trials, responding during CS+ was greater than during CS-. As measured by the percentage of CS+ probe trials with a CR, the difference between regular CS+ probe trials and CS- trials was reliable; $\underline{F}$ (1, 24) = 4.71. Thus, conditioning occurred with a US-CS-UR arrangement in which the CS preceded only the UR. The rate measure showed a similar trend on regular probe trials, but the difference between CS+ and CS- fell short of statistical significance; $\underline{F}$ (1, 24) = 3.03, $\underline{p} < .10$. Responding on CS- and Ctx trials did not differ for either the percentage or rate measure, $\underline{F}$s < 1.

During augmented probe trials in the US-CS-UR procedure in which CS+ was preceded by a 50-ms presentation of water, the difference in responding between CS+ probe trials and CS- trials increased substantially. (See the unfilled bars associated with CS+ and CS- in the middle sets of bars in both panels of Figure 4.) Responding during augmented CS+ probe trials exceeded CS- trials as measured by the percentage of probe trials with at least one TMR; $\underline{F}$ (1, 18) = 30.80; and the rate of TMRs; $\underline{F}$ (1, 18) = 32.27, respectively. Introducing a drop of water immediately prior to CS+ probe trials facilitated responding in the US-CS-UR procedure through more nearly reinstating the stimulus complex present on paired trials and, perhaps, through sensitizing the CR to an otherwise weak CS. To summarize, a forward CS-UR relation was sufficient to promote conditioning even when the CS-US relation was backward, especially when generalization decrement was reduced though the augmented probe-trial technique.

Some comment is in order concerning the absolute level of responding observed with the US-CS-UR procedure. The absolute level of responding was lower than the CS-US/UR arrangement of Experiment 1. This was anticipated because of the very brief CS-UR interval required to unconfound CS-US relations from CS-UR relations. The CS-UR interval in the US-CS-UR procedure was approximately 170 ms based upon the distribution of UR latencies (see Figure 2). The deleterious effect of such a brief interval on conditioning may be appreciated by considering the effect of a similarly brief CS-UR interval on NMR conditioning in the rabbit. In the NMR preparation, a CS-US interval of 250 ms (corresponding to a CS-UR interval of approximately 275 ms) produces very high levels of NMR responding—in the vicinity of 95%. However, if the CS-US interval is reduced to approximate the CS-UR interval of the US-CS-UR procedure in Experiment 2, the level of conditioned NMRs falls to about 30% (Smith, Coleman, & Gormezano, 1969). In short, even a preparation that otherwise supports high levels of conditioned responding yields quite low levels at the brief CS-UR interval required to separate the effects of CS-US and CS-UR relations. What is critical is not the absolute level of conditioning but its reliability, and this was satisfactory. Moreover, the absolute level of conditioning in the US-CS-UR procedure may underestimate the "true" level of conditioning: During acquisition, the CS occurred after a US of greater magnitude and after approximately 10% of the URs had begun. To the extent that these events contribute to the stimulus complex paired with the UR, some generalization decrement would occur even with the augmented probe technique.

Responding on augmented probe trials may be taken as evidence of conditioning only if a 50-ms water presentation did not, by itself, produce TMRs. To assess this possibility, we compared responding in post-conditioning sessions during trial periods following unsignaled 50-ms water presentations with equally long trial periods with Ctx alone. Responding during these two types of trials was very similar—11.1% versus 10.6% by the percentage measure and 0.33/s versus 0.51/s by the rate measure. These differences were unreliable, Fs < 1. Thus, a 50-ms water presentation did not by itself evoke TMRs.

US-UR-CS procedure. During training with the US-UR-CS procedure, CS+ followed the onsets of both the US and the UR thereby permitting only CS-UR overlap. The rightmost sets of bars in Figure 4 depict performance during this procedure as assessed by the percentage measure (upper panel) and the rate measure (lower panel). The differences in responding between CS+ and CS- were small during both regular and augmented probe trials, although responding during CS+ was routinely slightly higher. During regular probe trials, the difference between CS+ and CS- responding was nonsignificant as measured by both the percentage and rate of TMRs; Fs < 1. During augmented probe trials, the difference between responding during CS+ and CS- increased somewhat but remained short of statistical significance by both measures; Fs (1, 18) = 2.49 and 2.51, respectively, ps < .25. During CS- and Ctx trials with the US-UR-CS procedure, the percentages and rates of TMRs did not differ reliably, but were especially elevated relative to the corresponding values for the CS - - US-UR procedure in which CS+ preceded both the US and UR. When US presentations are unsignaled, Ctx provides the sole stimulus that is contiguous with the UR.

The absence of a reliable increase in CS+ responding with the US-UR-CS procedure weakens efforts to attribute responding in the US-CS-UR procedure to factors other than the ordinal relation of the CS to the UR. For example, it might be argued that the persistence of the US in the form of water remaining in the oral cavity permitted some portion of CS+ to precede or overlap some portion of the US, and that this conjunction of stimuli was responsible for conditioning in the US-CS-UR procedure (cf. McNish et al, 1997, p. 52, footnote 2). But, the same putative CS-US relation occurred in the US-UR-CS procedure where evidence of conditioning was lacking. Also, it might be argued that the drop of water given before augmented probe trials potentiated responding through some means other than reinstating the context in which conditioning took place. But, responding in the US-UR-CS procedure did not reliably increase on augmented probe trials when any such factors could presumably also operate.

Experiment 3

The results of Experiment 2 are consistent with the view that the temporal relation between the CS and UR is the critical operationally defined relation in TMR conditioning. This conclusion does not deny that variations in the CS-US relation affect conditioned performance, but invites the conjecture that such effects are the result of concomitant, confounded changes in the temporal relation of the CS to the UR. The importance of the CS-UR relation is supported by the finding that conditioning occurred whether or not the CS preceded the US so long as the CS preceded the UR. Conditioning occurred when the CS preceded the US and did not overlap the UR (the CS - - US-UR procedure) and when the CS followed the US but preceded and overlapped the UR (the US-CS-UR procedure). However, when the CS followed the onsets of both the US and UR and merely overlapped the UR (the US-UR-CS procedure) no reliable increase in conditioned responding was observed. In short, a forward CS-UR relation was both necessary and sufficient for responding to the CS; a forward CS-US relation was not necessary; and CS-UR overlap was neither necessary nor sufficient.

The conclusion that CS-UR overlap does not by itself promote conditioning must be tempered, however, even beyond the usual strictures against accepting the null hypothesis. First, on augmented probe trials in the US-UR-CS procedure, responding during CS+ exceeded CS- for all subjects as measured by both the percentage and rate of responding, although the differences were numerically small and variable. Second, generalization decrement—even on augmented probe trials—is more likely to occur in the US-UR-CS procedure than in the other procedures: Augmented probe trials do not fully reinstate the stimulus complex present on paired trials because the 50-ms water presentation only partially reproduced the sensory effects of the US and any sensory feedback from URs was absent altogether because the 50-ms water presentation did not evoke TMRs. Third, to the extent that the US-UR-CS procedure fostered conditioning to contextual stimuli, conditioning to CS+ could be blocked (Randich & LoLordo, 1979; Rescorla & Wagner, 1972). Thus, the possibility remains that CS-UR contiguity may support conditioning when assessed under more favorable circumstances (cf. Miller & Barnet, 1993; Rescorla, 1981).

To investigate further the contribution of contiguity between the CS and UR, we implemented a procedure in which overlap between the CS and the UR was varied, but in a manner that reduced the potential for generalization decrement and context blocking. The effects of CS-UR overlap were studied using extended–CS procedures in which the ISI was held constant but the CS continued for various times after the onset of the long-duration TMR, thereby increasing the amount of CS-UR overlap. Because extended-CS procedures also necessarily increase the total duration of the CS, additional conditions were instituted in which the CS durations were the same as those of the extended CS procedures, but in which the ISI was varied (cf. Schneiderman, 1966). That is, the effects of delay conditioning were examined.

CS extension has been previously studied using other conditioning preparations and the results have varied dependent, at least in part, on the duration of the UR. In general, when USs elicit brief URs—such as the shock-elicited NMR, eyelid response, and leg flexion—extending the CS after the US has a deleterious effect on conditioning (e.g., Barnes, 1956; McNish et al, 1997; Schneiderman, 1966; Wagner & Brandon, 1989). Contrariwise, when the US elicits long-duration URs, such as salivary responses in the dog or water-elicited JMRs in the rabbit, conditioning is facilitated (Konorski, 1948/1968, pp. 135-136; Sheafor, 1975). Facilitation has also been reported when an extended CS is employed with USs that may be presumed to elicit long-duration URs, such as shock-elicited autonomic responses. Under such circumstances, extended CSs have been shown to support acquisition of conditioned responses (Champion, 1962), to facilitate acquisition of another conditioned response (Kehoe, 2000), to facilitate conditioned suppression relative to other procedures (Albert, Ricker, Bevins, & Ayres, 1993; Ayres et al, 1987), and to facilitate reflexive responding (McNish et al, 1997). This pattern of findings is consistent with the proposition that CS-UR contiguity promotes conditioning. If CS-UR contiguity promotes conditioning, then extending the CS with long-duration URs constitutes an acquisition procedure because CS-UR overlap is increased. However, when the UR is of brief duration, extending the CS implements an extinction procedure because the extended portion of the CS is not paired with the UR.

Method

Subjects. Twenty-eight experimentally naïve pigeons served as subjects in Experiment 3 under the same water- and food-deprivation conditions as in preceding experiments.

Apparatus. The same experimental chambers, restraint apparatus, stimulus-producing devices, and response-monitoring devices were used in Experiment 3 as in Experiment 2.

Procedure. Subjects were randomly assigned to one of seven groups of four subjects each. For all groups, a differential conditioning procedure was used with the injection of 200-ms of water into the oral cavity as the US.

The effects of CS-UR overlap were studied using three groups for which the ISI was always 500 ms followed by a 200-ms US, but in which CS+ had durations of 700, 850, or 1,750 ms. Within each group, the duration of CS- was the same as CS+. Hereafter, these groups are designated E-0, E-150, and E-1050, respectively, to indicate the ms by which CS+ was extended past US offset. Based on the UR latency distribution (see Figure 2), the expected values of the overlap between CS+ and the UR during the extended portion of CS+ was 34 ms, 121 ms, or 852 ms, respectively. (The expected value of CS-UR overlap is the cumulative product of the probability that a bout of URs began during successive 50-ms post-US intervals summed over the remaining portion of the extended CS.)

CS-US delay was studied using three groups in which the CS duration was 850, 1750, or 2,200 ms. For all delay groups, the US occurred in the final 200 ms of the CS. Hereafter, these groups are designated D-650, D-1550, and D-2000 corresponding to ISIs of 650, 1550, or 2000 ms. Note that the total CS+ and CS- durations for the D-650 and D-1550 delayed-conditioning groups were the same as those of the E-150 and E-1050 CS-extension groups used for the study of CS-UR overlap.

The final group of subjects received a 700-ms CS duration with a 500-ms ISI, but the assignment of colors to CS+ and CS- was reversed from that of the other group trained with these same conditioning parameters. The seventh group counterbalanced the assignment of colors to CSs and increased the number of subjects in the baseline reference condition for the effects of CS-UR overlap and ISI duration. The seven groups formed an incomplete factorial design with three levels of CS-UR overlap and four levels of CS-US/UR delay (ISI duration), with the two groups receiving a 700-ms CS occupying the intersection of the two factors.

In addition to the aforementioned between-subjects evaluation of the effects of CS-UR overlap, a within-subjects evaluation was also implemented in Experiment 3. Upon completion of original training, the D-650 and D-1550 groups were shifted to an extended CS condition in which the CS+ and CS- durations were increased by 150 ms following US offset. Thus, the CSs were extended for the same duration as the E-150 group.

For all groups, the training regimen was the same as Experiment 2. That is, each conditioning session consisted of 28, 3-s trial periods with 10 paired CS+-US trials, 2 CS+ probe trials (trials 6 and 20) during which CS+ was presented alone, 12 CS- trials, and 4 Ctx-alone trials during which no phasic stimulus was presented. The intertrial interval averaged 2 min. All subjects received 10½ sessions of training. Subjects in groups D-650 and D-1550 received an additional 10½ sessions during which CS+ and CS- were extended. At the conclusion of training, each subject was given four sessions in which the 200-ms US was presented alone. Data from the four US-alone sessions contributed to the latency distribution of URs shown in Figure 2. The experiment was conducted in two sets of fourteen subjects, each set consisting of two animals from each of the seven conditions. The criteria used to score TMRs were the same as in Experiment 2.[2] The reliability of findings was assessed with analysis-of-variance techniques followed by planned comparisons using error terms appropriate for the effects being compared (Winer, 1971).

Results and Discussion

Before examining the effects of the independent variables of primary interest—CS-UR overlap and CS-US delay—we describe general characteristics of discriminative conditioning with these procedures. For the two E-0 groups, in which color was counterbalanced, the discrimination between CS+ and CS- was very similar and did not interact with the color assignment as measured by either the percentage or rate measure; Fs (1, 21) < 1 and 1.64, p > .25, respectively. Accordingly, performance of the two E-0 groups was combined in subsequent comparisons. Considering all groups, responding was greater during CS+ than during CS- (see Figures 5 and 6). These overall differences were reliable as measured by the percentage of trials with a TMR; F (1, 21) = 168.18; and the rate of TMRs; F (1, 21) = 35.39. (The performance of individual groups is considered shortly.) Turning to responding during trial periods in which only Ctx was present, responding during Ctx was typically slightly below CS- responding. Over all seven groups, the mean percentages and rates during Ctx were 7.2% and 0.21 TMRs/s, which was somewhat less than the corresponding values during CS-. The difference between CS- and Ctx responding was reliable as measured by both percentages and rates of TMRs; Fs (1, 21) = 19.60 and 16.83, respectively. (See Figures 5 and 6 for the results of individual groups.)

The level of responding during CS- relative to Ctx bears indirectly on the hypothesis that the degree of UR overlap affects conditioning: In those procedures in which CS+ was not extended into the post-US period (the two E-0 groups and groups D-650, D-1550, and D-2000), URs had an opportunity to occur during Ctx to a greater degree than in those procedures in which CS+ was extended (groups E-150 and E-1050). For the former set, the mean percentage of responses during Ctx trials was 8.8% and, for the latter set, 3.2%. The corresponding mean rates were 0.21 TMRs/s and 0.19 TMRs/s. Thus, responding during Ctx was generally greater for groups in which CS+ terminated with US offset than for those in which CS+ was extended into the period where URs occurred. The effects of CS extension on Ctx responding were reliable by the percentage measure, but not the rate measure; Fs (1, 21) = 13.93 and < 1, respectively. This pattern of results is consistent with the proposition that increasing the overlap between Ctx and UR promoted context conditioning.

Effects of CS-UR overlap. The effect of pairing CS+ with the UR was directly evaluated by examining responding during the portion of CS+ prior to the onset of the US/UR. Two types of comparisons were provided by the experimental design—a between-subject comparison based on independent groups receiving different CS extensions and a within-subjects comparison based on subjects first conditioned without CS-UR overlap and then shifted to a CS extension of 150 ms.

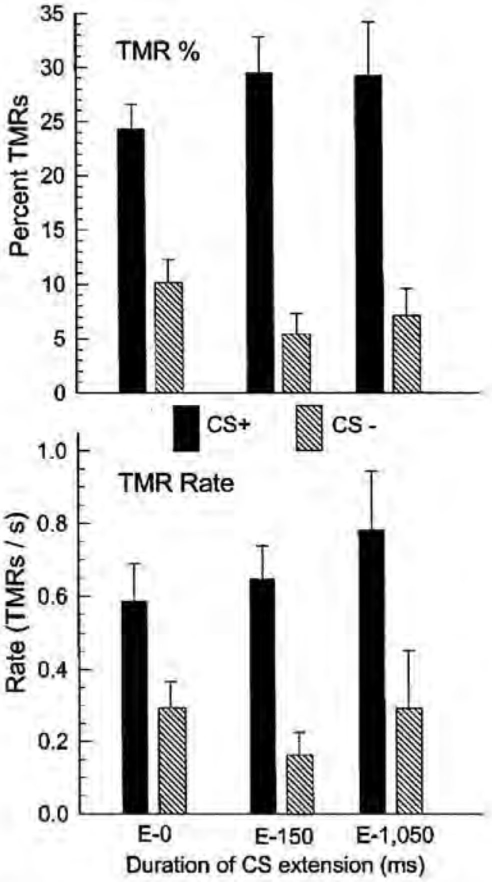

Figure 5. Effect on conditioning of the degree of CS-UR overlap produced by extending the CS after the offset of the US. For independent groups, the CSs were extended for 0 ms (E-0), 150 ms (E-150), or 1,050 ms (E-1,050). Solid-filled bars show responding during CS+. Bars with oblique lines show responding during CS–. Error bars indicate the standard error of the means. The upper panel shows the percentage of periods with at least one throat-movement response (TMR); the lower panel shows the rate of TMRs. CS = conditioned stimulus; UR = unconditioned response; US = unconditioned stimulus; CS+ = CS paired with the US; CS– = CS explicitly unpaired with the US.

Figure 5 shows that discriminative performance increased for the two groups that were trained with an extended CS (groups E-150 and E-1050) relative to the group without CS extension (E-0). As shown in the upper panel of Figure 5, CS extension increased the percentage of CS+ trials with a CR and had little systematic effect on performance during CS- trials. A similar pattern of findings occurred with the rate measure (see the lower panel of Figure 5). Thus, the change in discriminative responding was due almost entirely to an increase in responding during CS+. Statistical analyses supported these conclusions. Based on the percentage measure, discrimination performance measured by the difference between CS+ and CS- responding was greater for the E-150 and E-1050 groups as a set than for the E-0 group as shown by the stimulus x extension interaction; F (1, 21) = 4.40. Discrimination performance of the two groups trained with an extended CS did not differ; F < 1. Based on the rate measure, the interaction effect of stimuli with groups also indicated that the difference in responding between CS+ and CS- was greater for the set of two groups in which the CS was extended than for the E-0 group; F (1, 21) = 5.63. Again, the discriminative performance of the two extended groups did not differ, F < 1.

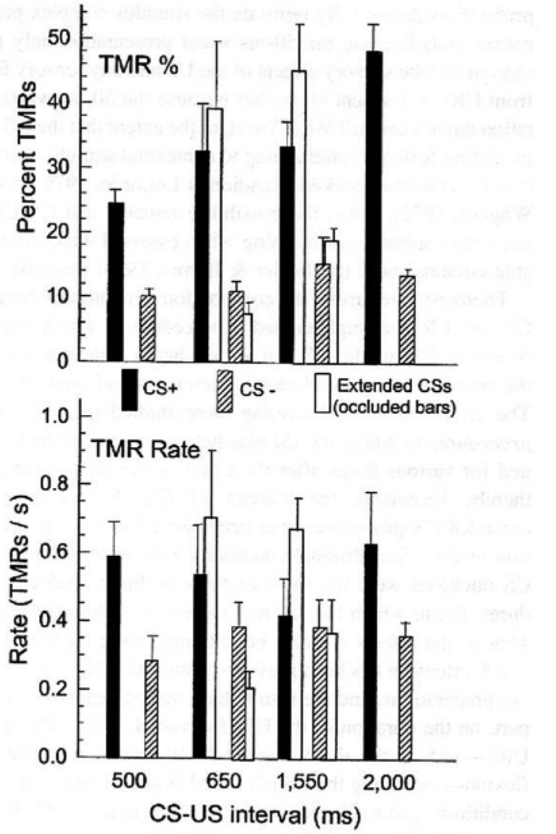

Figure 6. Effects on conditioning of the CS-US interval and of extension of the CS after the US-UR. Performance is shown for independent groups in which CS+ preceded the US by 500, 650, 1,550, or 2,000 ms. Solid-filled bars show responding during CS+. Bars with oblique lines show responding during CS–. Unfilled bars that are partially occluded by filled bars show responding during CS+ and CS– when the groups trained with interstimulus intervals of 650 or 1,550 ms later received a CS extension of 150 ms. Error bars indicate the standard error of the means. The upper panel shows the percentage of periods with at least one throat-movement response (TMR); the lower panel shows the rate of TMRs. CS = conditioned stimulus; US = unconditioned stimulus; UR = unconditioned response; CS+ = CS paired with the US; CS– = CS explicitly unpaired with the US.

The conclusion that increasing the CS-UR overlap improved discriminative conditioning was also confirmed by the within-subjects comparisons. As shown in Figure 6, extending the CS by 150 ms improved discriminative performance for the D-650 and D-1,550 groups relative to their prior performance when the CS coterminated with the offset of the US. When the CS was extended, the difference between responding during CS+ and CS- increased for both delay groups (see the partially occluded, unfilled bars in Figure 6) relative to when the CS coterminated with the US (the corresponding filled bars). This improvement occurred whether measured by the percentage of trials with a TMR (upper panel) or the rate of TMRs (lower panel). The change in discriminative performance was again primarily due an increase in responding during CS+ with no systematic effect on CS- responding. Statistical analyses supported these conclusions. The difference between CS+ and CS- increased reliably when CS-UR overlap increased as measured by the percentage of trials with a TMR; F (1, 6) = 9.23. The improvement in discriminative performance did not differ for the two delay groups; F < 1. Discriminative conditioning was also enhanced as measured by the rate of TMRs during CS+ and CS-; F (1, 6) = 57.42; and, again, did not differ for the two delay groups; F (1, 6) = 1.71, p > .25.

In summary, the between-subjects and within-subjects comparisons from Experiment 3 both indicated that CS-UR overlap promoted conditioning when the overlap was increased by extending the CS past the US into the period where URs occurred. Thus, the present findings join those of other studies in demonstrating that extending the CS past the US facilitates conditioning when the UR is a temporally extended response. The presence of a facilitatory effect of CS-UR overlap with the forward CS-US/UR procedure of Experiment 3 suggests that the absence of a reliable effect of CS-UR overlap in the US-UR-CS procedure of Experiment 2 was due to generalization decrement. That is, any beneficial effect of CR-UR overlap in the US-UR-CS procedure of Experiment 2 was partially offset by the adverse effects of a change in the context in which CS+ appeared between training and testing.

Effects of CS-US delay. We now consider performance when different delays occurred between the onsets of CS+ and the US/UR. The primary purpose of implementing different CS-US delays was to provide a control for CS duration when interpreting the effects of CS extension on conditioning: Increasing the CS-UR overlap also necessarily increased the duration of the CS. As shown in Figure 6, the percentage of trials with a TMR (upper panel) indicated that the difference between responding during CS+ and CS- became greater as the delay interval increased from 500 ms to 2,000 ms. The change in performance was primarily due to an increase in the percentage of CS+ trials with a TMR; responding during CS- did not vary systematically. Statistical analyses supported these conclusions. The stimulus x delay interaction was reliable; F (3, 21) = 5.28. Note, however, that there was no corresponding effect of CS-US/UR delay on the rate measure (bottom panel, Figure 6); F (3, 21) = 1.14, p > .25. The absence of an effect on the rate of TMRs differs from the general pattern of prior results in which changes in rate and percentage of TMRs covaried.

The difference in the pattern of findings for the percentage and rate measures suggests that the increase in the percentage of trials with a CR may not reflect an increase in conditioned strength when the CS-US/UR delay was increased. Consistent with this interpretation, groups E-150 and E-1050 received the same CS durations as groups D-650 and D-1550 but, when discriminative performance of these two sets of groups was compared, the difference in the percentage of TMRs between CS+ and CS- was larger for the set with an extended CS than for the set with a delayed CS as measured by the stimulus x sets interaction; F (1, 21) = 8.73. The significant interaction was due primarily to an increase in the percentage of responses during CS+ for the set with increased CS-UR overlap relative to the set with an increased CS duration: F (1, 21) = 7.46. The percentage of responses during CS- did not differ between the two sets; F (1, 21) = 2.09, p < .25. Thus, CS duration alone does not appear to account for the difference.

How, then, may we interpret the increase in the percentage of CS+ trials with a TMR as the delay interval increased (Figure 6, upper panel) together with the absence of a corresponding increase in the rate of TMRs (Figure 6, lower panel)? Among the factors may be the greater duration over which the CR was measured when the CS-US interval was increased from 500 ms to 650 or 1,550 ms relative to when the CS-US interval remained constant at 500 ms and CS duration was increased by post-US extension. Given the commonly found tendency of CRs to emerge after a constant proportion of the CS-US interval has elapsed, the delay procedures provided an increased opportunity for a bout of TMRs to begin (e.g., Smith, 1968). In addition, generalization of conditioned responding from the portion of the CS that was temporally contiguous with the UR to earlier portions of the CS would be greater with longer delays because the functional stimulus during successive moments within a delay interval increasingly resembles neighboring components of the CS as the delay interval lengthens, (e.g., Kehoe et al, 1993). Otherwise differing theoretical accounts of the time of emergence of CRs concur that proportional timing is approximated within periods of constant external stimulation prior to a US (cf. Gibbon & Church, 1990; Donahoe & Burgos, 1999; Moore & Choi, 1997; Staddon & Higa, 1996).

Experiment 4

The findings of Experiments 2 and 3 are most parsimoniously interpreted to indicate that the relation of the CS to the UR, not the US, is the critical, operationally defined, temporal relation in Pavlovian conditioning. That is, at the behavioral level of observation the second term in the two-term CS-US contingency of the Pavlovian procedure is functionally better indexed by the occurrence of the UR than the US. The strength of conditioning may be underestimated, however, when responding is assessed during the nominal CS because generalization decrement occurs between training and testing: When CS-UR pairings are simultaneous, the CS necessarily occurs in the context of the US and, perhaps, the stimulus consequences of the UR as well. Thus, following training with simultaneous CS-UR pairings, the stimulus context in which the UR occurred is not fully reinstated by the nominal CS. Additional test procedures, such as the augmented probe trials used in Experiment 2 or transfer tests may be required to reveal the full effects of simultaneous CS-UR pairings (cf. Rescorla, 1980).

The purpose of Experiment 4 was to characterize more precisely the nature of the critical events in the CS-UR relation. Prior experiments varied the relation of the CS to the UR and, perforce, to whatever other post-US behavioral and neural processes were correlated with the UR. A possible construal of these post-US processes is that they included lingering sensory consequences of the US. According to this view, the critical conjunction of events is between the CS and the inferred sensory consequences of the US that might result from water remaining in the oral cavity (or esophagus, or stomach, or intestine for that matter), and not processes related to the evocation of the UR per se. This view raises the possibility that the experimentally demonstrated effect of the CS-UR relation is of operational significance, but does not reveal a fundamental aspect of the conditioning process itself.

The possibility that post-US motor processes are confounded with post-US sensory processes—and that it is the latter that are critical—can be evaluated on both logical and experimental grounds. Logically, unless methods are devised that can separate CS-US relations from CS-UR relations, the proposal is tantamount to conceding that post-US sensory processes and post-US motor processes are inescapably confounded at the behavioral level of observation. Thus, the proposal preserves the view that the CS-US relation is critical for Pavlovian conditioning, but at a cost—the proposition becomes immune from direct experimental test at the behavioral level. In short, it becomes largely a matter of theoretical taste whether one describes the critical relation as between the CS and US, or between the CS and UR. On this view, the conventional emphasis on the CS-US relation may claim historical priority, but not logical or experimental priority over the CS-UR relation.

Experimentally, a test of the proposition requires that a means be identified whereby post-US sensory processes may be separated from post-US motor processes. This separation can be approximated with a US that evokes a temporally extended UR but that does not have enduring direct sensory effects. Experiment 4 sought to meet this objective by employing a puff of air to the oral cavity as the US instead of the injection of water. Prior research with rats has demonstrated that a water-deprived animal licks an air stream in much the same manner as a stream of water (Mendelson & Chillag, 1970). In preliminary work with pigeons, we found that a brief puff of air elicited an extended bout of throat movements. Thus, an air-puff US provides a means to separate more effectively post-US motor processes from post-US sensory processes. The claim that air remains in the ingestional system and provides distinctive post-US stimuli is considerably less compelling, although the possibility of lingering after-effects of the air puff cannot be eliminated. In Experiment 4, we used an air-puff US and varied the extent of CS-UR overlap through the extended-CS procedure of Experiment 3.

Method

Subjects. Six experimentally naïve pigeons served as subjects in Experiment 4 under the same schedule of water and food deprivation as previous experiments.

Apparatus. The same experimental chambers, restraint apparatus, stimulus-producing devices, and response-monitoring devices were used in Experiment 4 as in Experiments 2 and 3 except for implementation of the air-puff US. In addition, the counterweighted transducer arm was held against the throat by a 30 x 80 mm strip of paper coated with spirit gum to more faithfully track the smaller amplitude, more rapid TMRs associated with the tongue movements that accompany throat movements during swallowing (Zweers, van Pelt, & Beckers, 1981). To determine an appropriate US intensity, we conducted a preliminary study with three naïve pigeons that received three blocks of three US-alone sessions at each of three air-puff durations (50, 100, and 150 ms) in Latin-square order. The ITI was a variable 2-min as in prior work. Based on this study, a 50-ms air-puff US was selected that delivered 28.5 ml of compressed air though a 20-gauge hypodermic needle. Although the 50-ms air-puff was not presented enough times to characterize fully the distribution of TMR latencies, the median latency of a bout was 75 ms. The UR latency to the air-puff was less than to the water US, probably due to the high-frequency acoustic stimulus (a “hiss”) that accompanied the onset of the air puff and elicited throat movement as a component of a startle reflex. The duration of a TMR bout elicited by the air puff was similar, however, to the duration of the bout elicited by the injection of water (i.e., from 2 to 5 s). In summary, a 50-ms air-puff US evoked a bout of TMRs whose duration was sufficient to assess the effects of increased CS-UR overlap and whose immediate sensory effects did not persist (but whose lingering after-effects—if any—could, of course).

Procedure. Following two adaptation sessions, all six subjects were trained using a differential-conditioning procedure with a CS-US interval of 500 ms and a US of a 50-ms puff of air into the oral cavity. An ABA design was employed in which all subjects were first exposed to five sessions in which the CS was not extended after US offset, then five sessions in which the CS was extended for 1,050 ms after US offset, and finally five sessions in which the CS again terminated with US offset. Thus, Experiment 4 instituted a within-subjects test of the effects of CS-UR overlap, a method that provided a sensitive test of the effects of CS-UR overlap in Experiment 3. For all groups, the training regimen was the same as in Experiments 2 and 3. Each session consisted of 10 paired CS+-US trials, 2 CS+ probe trials (trials 6 and 20), 12 CS- trials, and 4 Ctx-alone trials with an average ITI of 2 min. The green stimulus served as CS+ and the red stimulus as CS-. The reliability of findings was assessed using analyses-of-variance for repeated measures followed by planned comparisons with error terms appropriate for the effects being compared (Winer, 1971).

Results and Discussion

The effects of using an air puff as a US instead of a squirt of water are shown in Figure 7 for the percentage measure (upper panel) and the rate measure (lower panel). Conditioning occurred with an air-puff US much as it had with a water US, except for the higher absolute rate of TMRs detected by the transducer because of improved monitoring of small, rapid throat movements. Discrimination occurred in all conditions as shown by greater responding during CS+ than CS- for both dependent measures.

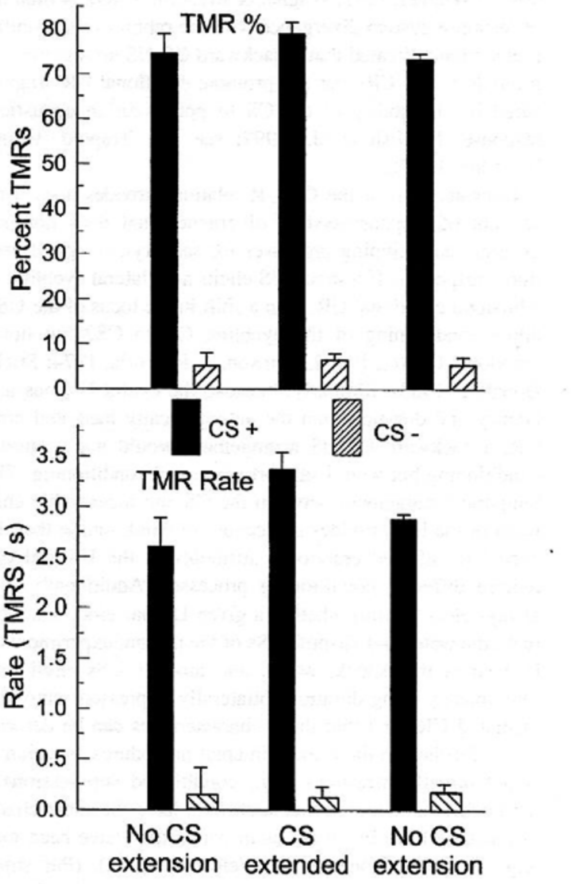

Figure 7. Effect of the extent of CS-UR overlap on conditioning with a 50-ms air puff as the US. Performance is shown for subjects that were first conditioned when CS+ and the US coterminated (no CS extension), then when CS+ was extended for 1,050 ms after US termination (CS extended), and finally when CS+ and the US again coterminated (no CS extension). Solid-filled bars show performance during CS+. Bars with oblique lines show responding during CS–. Error bars indicate the standard error of the means. TMR = throat-movement response; CS = conditioned stimulus; UR = unconditioned response; US = unconditioned stimulus; CS+ = CS paired with the US; CS– = CS explicitly unpaired with the US.

On the central point of the experiment, the discrimination between CS+ and CS- was facilitated by extending the CS past the offset of the US—thereby increasing CS-UR overlap. The difference in responding between CS+ and CS- increased when training was shifted from the nonextended to the extended condition and returned to approximately its previous level when

CS-UR overlap was again reduced. Statistical analyses supported these conclusions. The level of responding during CS+ was higher in the extended condition than in the nonextended conditions as assessed by both the percentage and rate measures; Fs (1, 5) = 10.96 and 29.19, respectively. Responding during CS- did not change systematically between the nonextended and extended conditions as assessed by either measure; Fs < 1. Responding during both CS+ and CS- did not differ between the two nonextended conditions by either measure; all Fs < 1 except for the rate measure during CS+; F (1, 5) = 4.19, p < .10. This pattern of results caused the interaction of stimuli (CS+ vs. CS-) with conditions (extended vs. nonextended) to be reliable by the rate measure; F (1, 10) = 17.02 and to fall just short of reliability by the percentage measure; F (1, 10) =3.38, p < .10. Taken together, the findings from Experiment 4 support the conclusion of Experiment 3 that CS-UR overlap promotes conditioning even when the immediate sensory effects of the US do not persist.

It is of interest that the absolute percentages of TMRs during CS+ were greater with the air-puff US than with the water US in Experiment 3. Direct comparisons are complicated because of uncertainties concerning the relative functional magnitudes of the two types of USs and changes in the monitoring of TMRs, but the finding is consistent with the view that conditioning occurs when the functional CS and UR are contiguous. When a UR has a shorter latency, as with the air-puff US, the stimulus complex with which the UR is paired is more nearly restricted to the nominal CS than when the UR has a longer latency, as with the water US. With a long-latency UR, the functional CS more likely includes stimuli characteristic of later aspects of the CS and—possibly—stimuli afforded by the US and UR as well. From this perspective, higher levels of responding during the nominal CS are anticipated when the US elicits short-latency URs, such as shock-elicited NMRs or air-puff-elicited TMRs, than when the US elicits long latency URs, such as water-elicited JMRs and TMRs (e.g., Smith et al, 1966) or autonomically mediated URs (e.g., McNish et al, 1997; Vandercar & Schneiderman, 1967).

General Discussion

The General Discussion considers some of the broader experimental and theoretical implications of these experiments.

In light of the present findings, the conventional view that the relation between the CS and US is the critical temporal relation in Pavlovian conditioning should be revisited. In terms of observable experimental events, the most parsimonious interpretation of the present results is that the critical temporal relation is between the CS and the UR, not the US. The proposition that conditioning is produced by simultaneous pairing of the functional CS with the UR is consistent with the occurrence of conditioning in the US-CS-UR procedure of Experiment 2 and the facilitatory effects of CS extension in Experiments 3 and 4.

The functional CS includes not only the nominal CS, but also the full stimulus complex that is contiguous with the UR. This conception of the CS is consistent with the unreliable increase in responding when the UR merely overlapped the CS in the US-UR-CS procedure of Experiment 2 and the reliable increase in responding when the CS overlapped the UR in the US-CS-UR procedure or appeared alone on paired trials in the extended-CS procedures of Experiments 3 and 4. The nominal CS incompletely specifies the functional CS in backward conditioning procedures and those that employ longer latency, longer duration URs.

Consideration of the CS-UR relation also provides a means to interpret differences in the asymptotic levels of conditioned responding and in the optimal ISIs found with USs that elicit URs of differing characteristics: As compared to USs that elicit long-latency, long-duration URs, USs that elicit short-latency, brief-duration URs should support higher levels of conditioned responding at shorter ISIs when assessed during the nominal CS. This is because the UR occurs soon after the onset of the nominal CS and concludes near its termination with a forward CS-US temporal relation and a short-latency, brief-duration UR. Such a temporal CS-UR relation minimizes conditioning to stimuli other than the nominal CS.

It should be re-emphasized that the possibility that the CS-UR relation can be a critical temporal relation in some instances of Pavlovian conditioning is not inconsistent with the ubiquitous finding that varying the CS-US relation affects conditioning: When the CS-US interval varies, the CS-UR relation necessarily varies concomitantly. Thus, the core empirical finding of the Pavlovian procedure is untouched by the present conclusion. What the present findings do question, however, is whether theoretical interpretations that emphasize the CS-US relation are required by demonstrations that conditioning varies with the temporal relation between the CS and US.

In addition to providing a basis for interpreting findings from the present experiment and differences in the level of conditioned responding with different URs, the CS-UR relation also provides a means for interpreting response-system divergences. Schneiderman (1972) proposed the term response-system divergence to designate cases in which different response systems exposed to the same CS-US training regimen are not similarly conditioned. For example, a shock US applied in the vicinity of the eye of a rabbit elicits both nictitating-membrane and cardiac responses as URs; however, the same CS-US interval is not equally effective in conditioning both response systems (Vandercar & Schneiderman, 1967). If conditioning depends on CS-US relations, then how are such differences to be understood? A number of other instances of response-system divergence have been identified more recently (e.g., Betts, Brandon, & Wagner, 1996; Tait & Saladin, 1986; Tait, Quesnel, & ten-Have, 1987; McNish et al, 1997). In one such study, the infraorbital region to which a shock US was applied in a rabbit eyelid-conditioning experiment was shifted to the contralateral eye between the two phases of a blocking design (Brandon, Betts, & Wagner, 1994). In phase 1, CS1 was paired with shock and, in phase 2, a simultaneous compound stimulus of CS1 and CS2 was paired with the same intensity of shock. Because shock elicits an unconditioned eyelid response preferentially in the ipsilateral eye, changing the locus of the US caused the UR to shift to the contralateral eye. When the locus of shock was shifted between phases 1 and 2, blocking of eyelid conditioning to CS2 failed to occur whereas, when the locus of eye shock remained the same (and, hence, the UR remained unchanged), conditioning to CS2 was blocked. This aspect of the study confirmed prior work with NMR conditioning in which a change in the locus of the US/UR eliminated blocking (Stickney & Donahoe, 1983). The finding of present interest is that—in contrast to the effects of changing the locus of shock on eyelid conditioning—a shift in the locus of the US did not promote conditioning of what was termed an “emotional” response to CS2. Emotional conditioning was assessed by the ability of CS2 to potentiate a startle response to an acoustic stimulus. The differential effect of a shift in US locus on eyelid and emotional conditioned responses exemplifies a response-system divergence. This response-system divergence was attributed to a difference in conditioning processes for “sensory-perceptual” versus “emotional attributes” of the US (McNish et al, 1997, p. 50-51; Wagner, 1981; Wagner & Brandon, 1989). A final instance of response-system divergence with the rabbit eyelid-conditioning preparation indicated that a backward CS-US arrangement did not promote eyelid CRs but did promote emotional CRs (again measured by the ability of the CS to potentiate an acoustic startle response) (McNish et al, 1997; see also Trapold, Homzie, & Rutledge, 1964).

Consideration of the CS-UR relation provides a parsimonious account of response-system divergence that does not postulate different conditioning processes for sensory-perceptual and emotional responses. If a shock US elicits a unilateral eyeblink UR but a bilateral emotional UR, then a shift in the locus of the US would allow conditioning of the eyeblink CR to CS2 but not of the emotional CR (cf. Bakal, Johnson, & Rescorla, 1974; Stickney & Donahoe, 1983). Similarly, because the eyelid UR has a shorter latency and duration than the autonomically mediated emotional UR, a backward CS-US arrangement would not support eyelid conditioning but would support emotional conditioning. Thus, the temporal arrangement between the CS and measurable characteristics of the UR provides an account of conditioning that does not appeal to inferred emotional attributes of the US and does not require different conditioning processes. Additionally, it is not always clear a priori whether a given US has "emotional attributes;" e.g., the water and air-puff USs of the present experiments. What is clear is that shock, water, and air-puff USs elicit relatively long-latency, long-duration, bilaterally expressed, autonomically mediated URs and that these characteristics can be determined a priori. Further, in those experimental procedures in which the UR is not directly measured, e.g., conditioned suppression, it can reasonably be assumed that such URs have the same characteristics as they have in situations in which they <u>have</u> been measured (e.g., Borgealt, Donahoe, & Weinstein, 1972). (Put simply, an event can occur whether we measure it or not.) The assumption that USs elicit URs when the URs are not directly measured seems less fraught with difficulties than appeals to inferred stimuli whose characteristics may be adjusted to accommodate the phenomena they seek to explain.

Consideration of the CS-UR relation need not negate the contributions of theoretical accounts of conditioning that are now stated in terms of CS-US relations. As a case in point, the present pattern of findings can potentially be accommodated by a judicious choice of parameters in Sometimes-Opponent-Process (SOP) theory (Wagner, 1981; Wagner & Brandon, 1989). In SOP theory, excitatory conditioning is asserted to occur when (stated briefly) two hypothetical stimulus elements—CS elements and activated US elements—co-occur. If US elements are assumed to be activated for as long as the UR occurs (i.e., their activation is not restricted to the duration of the operationally defined US), then SOP theory—supplemented by generalization decrement—might accommodate the findings with both the US-CS-UR procedure of Experiment 2 (a backward CS-US relation) and the extended CS procedures of Experiments 3 and 4 (increased CS-UR overlap). However, note that if US elements are assumed to be in an active state for the duration of the UR, then the experimental distinction between CS-US and CS-UR relations becomes moot: The hypothesized US elements could be designated—with equal justification—<u>UR</u> elements (see McNish et al, 1997). The interpretation of the hypothetical elements as US elements could be maintained by claiming that the fundamental relation is between the CS and US-instigated <u>stimuli</u> that accompany the UR. However, this claim asserts a theoretical preference for an <u>inferred</u> US over an <u>observed</u> UR. If inferred events are to be introduced, they can as readily be construed as inferred response elements as inferred stimulus elements.

The conclusion that the temporal relation between the CS and UR is fundamental in at least some instances of Pavlovian conditioning should be evaluated for its generality in other conditioning preparations. Clearly, it has long been recognized that the behavioral expression of the UR is not necessary for conditioning as demonstrated by cases in which the behavioral UR is prevented (as when transmission at the neuromuscular junction is blocked; e.g., Solomon & Turner, 1962) or by cases in which the CS does not support expression of the UR (as when an auditory CS is paired with food for the pecking response of the pigeon; e.g., Leyland & Mackintosh, 1978). However, if the behavioral expression of conditioning were not highly correlated with the neural mechanisms that mediate conditioning, then those mechanisms could never have been naturally selected. As E. O. Wilson has observed, "learning is the pacemaker of evolution" (Wilson, 1975). Nevertheless, once these mechanisms have been naturally selected, their behavioral expression is not necessary for the environment to engage them. Preparations that employ USs that elicit measurable URs of relatively long latency and duration, such as the rabbit JMR, or that directly measure URs presumed to have these characteristics, such as the autonomic responses accompanying conditioned suppression and NMR conditioning, should be especially informative. Most importantly, perhaps, the possibility that CS-UR relations play a key role in Pavlovian conditioning encourages efforts to formulate a unified theoretical treatment of conditioning that applies equally to Pavlovian and instrumental procedures (cf. Hilgard & Marquis, 1940; Kintsch & Witte, 1962; Shapiro & Miller, 1965). Both conditioning procedures produce a change in the environmental control of behavior—most notably the UR in Pavlovian procedures and the R in addition to the UR in instrumental procedures (Donahoe, 1997, 2002; Donahoe, Burgos, & Palmer, 1993; Donahoe & Palmer, 1994; Donahoe, Palmer, & Burgos, 1997).

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Footnotes

[1] The onset times and durations of stimuli were measured directly at the stimulus-producing devices. The stimulus times reported in the body of the text are the nominal times that were programmed by the computer. For direct measurements, the onset of the CS was detected by a phototransistor positioned in front of the CS display cell. The direct measurement of the onset of the US was detected by two electrodes placed in the US water stream at a distance of 5 mm from the opening of the cannula, which approximated the distance from the tip of the cannula to the floor of the oral cavity. Contact of water with the tongue and floor of the mouth initiates the sequence of responses comprising the swallowing reflex (Zweers, van Pelt, & Beckers, 1981). The voltages from the electrodes were monitored by the same A/D converter used to monitor

throat movements. The obtained difference in onset times between the CS and US was 13 ms more than the programmed difference implemented by the computer; e.g., a nominal ISI of 500 ms was actually 513 ms. The obtained duration of CSs was 116 ms longer than the programmed value because of the time required for the lamp filaments to cool. The duration of the US was within 10 ms of the programmed duration of 200 ms. The relation of TMRs to stimuli reported in the text was measured from the actual times of occurrence of stimuli, not their nominal programmed times.

[2] Experiment 3 reports findings from a dissertation submitted by the second author in partial fulfillment of requirements for the Ph.D. at the University of Massachusetts (Vegas, 1995). In the portion of the dissertation describing these findings, an erroneous constant was entere computer program used to score TMRs. The error was corrected here and the data rescored. The primary findings of the dissertation were qualitatively unchanged.

Fig. 1