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CS-US Interval Duration and the US-Preexposure Effect

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Three experiments examined the role of CS (conditioned stimulus) duration in the unconditioned stimulus (US) preexposure effect. Rats received preexposure to unsignalled food pellets that were delivered on a fixed-time 90-s schedule and magazine entry responses were recorded. In Experiment 1, there was no evidence of retardation of conditioning to a 15- or 60-s CS when rats that received US preexposure were compared to unexposed control groups. Experiment 2 revealed a US-preexposure effect with a 90-s CS, but only when the rats were given a 31.5-min wait in the experimental chambers prior to the onset of US exposure. In Experiment 3, it was discovered that the magnitude of US preexposure was related to CS duration, with longer CS durations demonstrating progressively greater retardation in conditioning. The results are discussed in light of recent time-based accounts of classical conditioning.

Preexposure to an unsignalled US (unconditioned stimulus) can produce an attenuation of conditioning to a CS (conditioned stimulus) that is paired with the US in a subsequent stage of training. One interpretation of this phenomenon, known as the US-preexposure effect, is that it is an instance of blocking. It has been argued that initial exposure to the US results in the formation of an association between features of the experimental context in which the US was presented and the US (e.g., Baker et al., 1981; Hinson, 1982; Tomie, 1976a, 1976b). The context then blocks acquisition to a discrete CS in much the same way that one discrete CS might block another discrete CS (Kamin, 1969). Although much of the focus of US-preexposure research has been on the role of context-US associations, there is some evidence indicating that interval durations play an important role in the US-preexposure effect. Mean US-US interval has a robust effect on the magnitude of the US-preexposure effect, with shorter US-US intervals producing a bigger decrement in conditioning to the CS (Balsam et al., 1980; Goddard & Jenkins, 1988).

It also appears important that the US-US interval given in the preexposure phase is maintained during CS-US training. Using pigeons in an autoshaping preparation Goddard and Jenkins (1988) gave preexposure to food US-US deliveries that were separated by either a short (10.5 s) or a long interval (100.5 s). During the CS-US training phase, the US-US interval was either maintained as short or long, or shifted to the other duration. Shifting the US-US interval resulted in an alleviation of the US-preexposure effect to a 10-s keylight CS that was paired with the US so that performance in the shifted groups was similar to untreated controls. In an extension of these findings, Williams and LoLordo (1995) gave rats a single daily shock either 120 s or 1200 s after being placed in an experimental context.

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The rats then received a 30-s CS that was paired with the US, but the US occurred at 120 s in all groups so that the time of US delivery was altered for the 1200-s group. They also manipulated the context so that half of the rats experienced a context change during CS-US training whereas the other half received training in the original context. They found that the US-preexposure effect was evident only in groups that had the time of US delivery held constant and that the context manipulation had no effect.

A third temporal variable of importance is variability of the US-US interval, with increasing variability leading to a weakening of the US-preexposure effect. This effect has been observed with the addition of long intervals to a normally short US-US interval (Goddard & Jenkins, 1988) or by adding both longer and shorter intervals and holding the mean constant (Kirkpatrick & Church, 2000a). The effect also occurs whether variability is present throughout both preexposure and conditioning phases (Kirkpatrick & Church, 2000a), or only added during the preexposure phase and then removed during the conditioning phase (Goddard & Jenkins, 1988) suggesting that the effect of variability is on initial learning of the US-US interval during the preexposure phase.

Thus, it appears that a maximal interference in CS conditioning will occur with US-preexposure treatment if the US-US interval is a short fixed duration and the US-US interval during CS-US training is the same as in the preexposure phase. The time-of-arrival hypothesis (Goddard & Jenkins, 1988) states that a US can potentially signal the time of delivery of the subsequent US and in this manner the US itself reduces the surprise value of subsequent US presentations (see also Egger & Miller, 1963). The hypothesis also predicts that an essential component of the US-preexposure effect is the maintenance of the US-US interval between the preexposure and CS-US training phases. Moreover, shorter US-US intervals would produce a more robust preexposure effect because shorter intervals are timed more accurately. Similarly, adding variability to the US-US interval would reduce the ability of prior USs to predict the time of arrival of the next US because a reduction in timing accuracy.

Conventional accounts of US preexposure (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972) have difficulty predicting the effect of temporal variables on conditioning in US-preexposure experiments. For example, these theories do not predict any effect of added variability on context conditioning provided that the mean US-US interval is held constant. Kirkpatrick and Church (2000a) held mean US-US interval constant and found that added variability alleviated the US-preexposure effect. Therefore, it appears that the time-of-arrival hypothesis provides the best prediction of the three known effects of temporal variables on the magnitude of the US-preexposure effect.

One temporal variable that has been overlooked is the role of CS duration. One reason for a lack of interest in this temporal variable may be that earlier theoretical accounts predicted no effect of CS duration on the magnitude of the US-preexposure effect. According to the time-of-arrival hypothesis, the predictability of the upcoming US by the prior US is not affected by the duration of the CS (however, the *relative waiting time hypothesis* proposed by Jenkins, Barnes & Barrera, 1981 could be applied to take CS duration into account). Likewise, contextual conditioning accounts also predict no effect of CS duration on context blocking (Baker et al., 1981; Hinson, 1982; Tomie 1976a, 1976b).

More recently, Gallistel and Gibbon (2000) have proposed rate expectancy theory (RET), which supposes that the speed of conditioning is determined by a comparison of perceived rates of reinforcement in the CS (T) and background (I). RET does predict an effect of CS duration on the magnitude of the US-preexposure effect. According to RET, the magnitude of US-preexposure effect will be determined by the I/T ratio. For any given US-US interval duration, shorter CS durations will result in a larger I/T ratio, which will increase the speed of conditioning to the CS. The I/T ratio will interact with US-preexposure treatment so that the preexposure effect will be diminished when I/T ratio is large; that is, larger I/T ratios overwhelm any effect of preexposure treatment and result in relatively normal speeds of conditioning to the CS. Thus, an investigation of the influence of CS duration on the US-preexposure effect would shed further light on the nature of the contribution of temporal variables to cue competition and would also allow for a further evaluation of current theoretical accounts.

The US-preexposure effect is a robust phenomenon that has been demonstrated in a wide variety of Pavlovian preparations (e.g. conditioned eyeblink response: Hinson, 1982; CER: Mowrer, 1987; conditioned taste aversion: Braveman, 1975; Gillan & Domjan, 1977; fear conditioning: Dickinson, Hall, & Mackintosh, 1976; pigeon autoshaping: Durlach, McQuoid, & Regehr, 1990; Goddard & Jenkins, 1988). To date, however, evidence for a US-preexposure effect using an appetitive conditioning procedure with rats has been quite limited. Timberlake (1986) found that preexposure to unsignalled food US presentations interfered with acquisition of contact responses to a ball bearing CS that was paired with food. However, we know of no published instances where US preexposure has interfered with goal tracking (magazine entry) responses in rats, despite the growing use of this paradigm for the study of conditioning processes. The present set of experiments attempted to establish the US-preexposure effect in the appetitive goal-tracking procedure with rats and determine whether the degree to which the CS fills the US-US interval contributed to the magnitude of the effect.

Experiment 1

Experiment 1 examined whether CS duration interacts with the US-preexposure effect. Separate groups of rats received US preexposure with a fixed 90-s food-food interval. The rats then received CS-US training with either a short (15 s) or long (60 s) CS that occurred at the end of the US-US interval.

Because all groups received the same duration US-US interval, any difference in the magnitude of the US-preexposure effect would most likely be due to CS duration, or perhaps some aspect of the relationship between the duration of the US-US interval and CS duration. If the US-preexposure effect is sensitive to the duration of the CS, then the effect should be greater in the group that received the long CS (compared to a no-treatment control group) than in the group that received the short CS.

Method

Animals. Twenty-four male Sprague Dawley rats (Harlan, UK) were housed in pairs in a colony room on a 12:12 h light:dark cycle (lights on at 08:00 h). The rats were fed a daily ration that consisted of 45-mg Noyes pellets (Improved Formula A) that were delivered during the experimental

session, and an additional 15 g of food given in the home cage shortly after the daily sessions. Water was available ad libitum in both the home cages and experimental chambers. The rats arrived in the colony at 35 days of age and were paired together so as to match their weights as closely as possible. They were handled daily until the onset of the experiments and were weighed weekly to check for adequate weight gain; all of the rats demonstrated normal growth curves throughout the experiment. Training began when they were 55 days old.

Apparatus. Each of the 12 chambers (25 x 30 x 30 cm) was located inside of a ventilated, noise-attenuating box (74 x 38 x 60 cm). A chamber was equipped with a food cup and a water bottle. A magazine pellet dispenser (Model ENV-203) delivered 45-mg Noyes (Improved Formula A) pellets into the food cup. Each head entry into the food cup was transduced by an LED-photocell. The water bottle was mounted outside the chamber; water was available through a tube that protruded through a hole in the back wall of the chamber. Two Pentium III 800-mHz computers running Med-PC for Windows (Tatham & Zurn, 1989) controlled experimental events and recorded the time at which events occurred with 2-ms resolution.

Procedure. The rats were randomly assigned to one of four groups: P15, U15, P60, and U60. There were two phases of training that composed the experiment: US preexposure and CS-US training.

US Preexposure (Sessions 1-10): During the preexposure phase, groups P15 and P60 received US-preexposure treatment with unsignalled food deliveries. The time between successive food deliveries was a fixed interval of 90 s. There were 70 food deliveries in each of 10 daily preexposure sessions. During this time, groups U15 and U60 were placed in the experimental chambers, but did not receive any CS or US deliveries. The houselight was on for the entire session in all groups.

CS-US Training (Sessions 11-20): Following US-preexposure treatment, 10 CS-US training sessions were conducted. All four groups received 70 CS-US pairings per session. The houselight was on for the entire session in all groups. The US-US interval was a fixed interval of 90 s, as in the preexposure phase. The CS was a 70 dB white noise that always occurred at the end of the US-US interval. Groups P15 and U15 received a 15 s CS and groups P60 and U60 received a 60-s CS. On a random 10% of the trials (probes), the time from the prior food until CS onset was lengthened to 180 s. The CS followed this 180 s period and the US was delivered at the end of the CS. The probes were given so as to uncouple timing of the US-US and CS onset-US intervals thereby allowing for an examination of: (1) responding to the US-US interval, measured in the absence of the CS; and (2) responding to the CS, with a minimal contribution from the prior US delivery.

Results

US Preexposure. The mean rate of responding during the US-US interval increased as a function of sessions of training during the preexposure phase from around 9 responses/min on Session 1 to around 15 responses/min by the end of training in both groups (data not shown). This was verified by an analysis of variance which disclosed a significant effect of sessions on mean response rates (over seconds 20-90 – the first 20 s were omitted because the rats were likely eating the previously delivered food pellet during this time as seen in Figure 1), $F(9, 90) = 5.3$, $p < 0.001$. Moreover, the analysis of variance (ANOVA) revealed that responding did not differ between the two preexposure groups, $F < 1$. The groups would not be expected to differ because they had received the same fixed 90-s interval during the preexposure phase.

Figure 1 contains the rate of head entry into the food cup in successive 5-s bins during the food-food interval, collapsed over the second half of the preexposure phase. Both groups displayed an initial high rate of responding, probably due to consumption of the food pellet, followed by a gradually increasing rate of responding as a function of time. The functions produced by the two groups did not

appear to differ in shape. Thus, both groups learned to time the fixed food-food interval during preexposure.

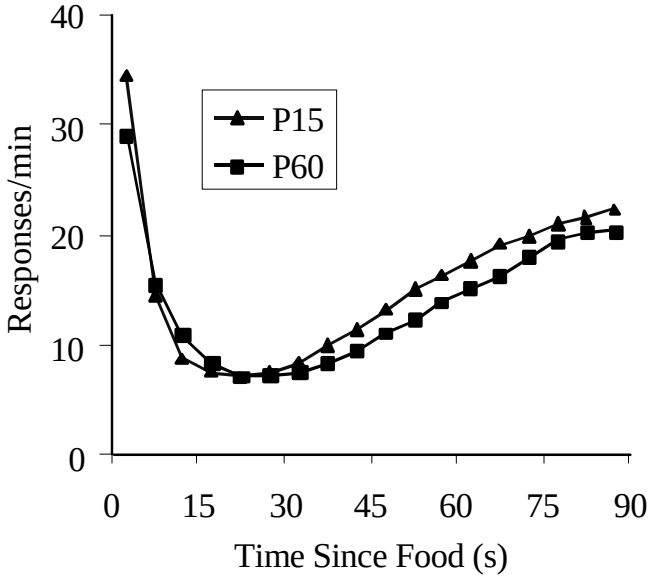

Figure 1. Response rate as a function of time since the prior food delivery during the preexposure phase of Experiment 1 for preexposed groups of rats.

CS-US Training. The response rate as a function of time is shown in Figure 2 for the probe trials, collapsed across the ten sessions of CS-US training. The probe trials involved the delivery of an empty 180-s interval followed by the CS and then food. Responding initiated by prior food delivery can be observed in the first 180 s of the probe, and responding initiated by CS onset can be observed following the break in each curve at 180 s (the time of CS onset). Responding was initially high due to consumption of the previously delivered food pellet. There was also anticipation of the next food delivery (which was omitted), which peaked at around 90 s and then decreased somewhat, but did not fall to zero. During the first 90 s of the probe trial, responding differed between the groups. Specifically, an ANOVA conducted on the mean response rates over seconds 20-90 of the probe revealed that the 15-s groups responded at a higher rate than the 60-s groups, $F(1, 20) = 9.2$, $p < 0.01$. Moreover, the unexposed groups responded more than the preexposed groups, $F(1, 20) = 8.1$, $p < 0.05$. There was no interaction of interval and preexposure condition, $F(1, 20) = 1.2$.

However, the difference among the groups was only observed during the first half of the empty portion of the probe trials; the groups had converged during the pre-CS period. An ANOVA on the mean rates of responding during the pre-CS period (the last 15 or 60 s of the empty portion of the probes for groups with 15 or 60-s CSs, respectively) revealed no effect of CS duration, preexposure, or their interaction, on responding, $F(1, 20) \leq 1.1$.

The second feature of the probe trials is that CS onset produced a sudden and profound increase in response rate. Responding then continued to increase throughout the CS, reaching a maximum just prior to the time of the next food delivery. Elevation scores are displayed in Figure 3 as a function of sessions of training. The elevation score was the rate in the pre-CS period subtracted from the rate

during the CS. The elevation scores increased as a function of training, $F(9, 180) = 5.9$, $p < 0.001$ and were higher for groups that received a 15-s CS than for groups that received a 60-s CS, $F(1, 20) = 18.6$, $p < 0.001$. Separate analyses conducted on the pairs of groups receiving the same CS duration revealed no evidence of a pre-exposure effect, Fs < 1.

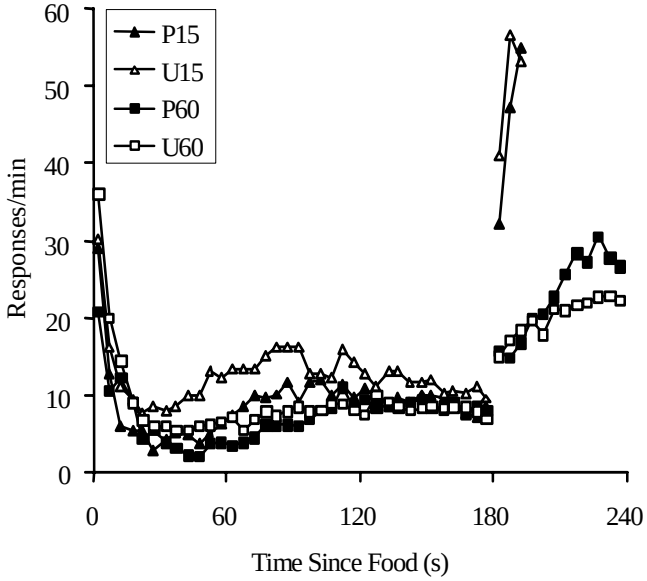

Figure 2. Response rate as a function of time since the prior food delivery during probe trials that were intermixed with CS-US training trials in Experiment 1. The time of CS onset is indicated by a break in each function.

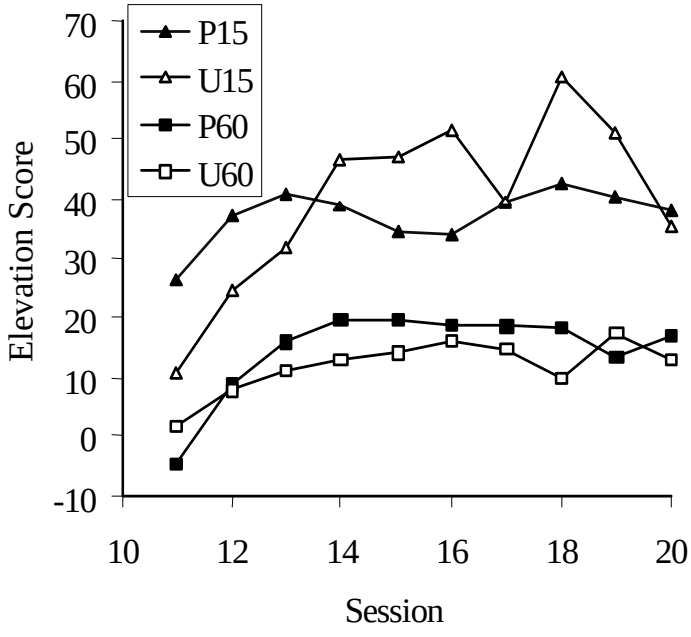

Figure 3. Elevation score (CS rate – pre-CS rate) as a function of sessions of CS-US training in Experiment 1.

Discussion

During the initial US exposure phase, rats demonstrated temporal conditioning to the fixed 90-s US-US interval (Figure 1), but this learning had no effect on their subsequent learning to respond to the CS when that CS was paired with the preexposed US. CS duration had no effect on whether the preexposure effect was observed, but did determine the rate of responding and shape of the response gradients. Groups with the 15-s CS demonstrated higher rates and more steeply increasing response rate functions during the CS (Figure 2).

According to RET (Gallistel & Gibbon, 2000), CS duration should have affected the magnitude of US preexposure. It was expected that the 60-s group should have demonstrated a noticeable retardation in conditioning, but the 15-s group was expected to show conditioning that was more similar to the control group. On the other hand, both context blocking (Baker et al., 1981; Hinson, 1982; Tomie 1976a, 1976b) and time of arrival (Goddard & Jenkins, 1988) accounts predict retardation of conditioning in both groups. Thus, the failure to observe a preexposure effect with either CS duration is somewhat disconcerting.

One factor that did differ among the preexposed and unexposed groups was the response during the empty portion of probe trials during the CS-US training phase, which was meant to assess learning of the US-US interval. The unexposed control groups showed a greater response during the first half of the empty portion of the probes compared to the preexposed groups. However, a closer examination of the form of responding in Figure 2 revealed that these differences were due to more accurate timing in the preexposed groups. The preexposed groups demonstrated less responding early in the US-US interval than the unexposed groups. The mostly likely source of the effect was the difference in amount of training with the US-US interval. The preexposed groups had received substantial training with the US-US interval prior to the onset of CS-US training and thus appeared to have learned to inhibit responding early in the US-US interval compared to unexposed groups.

The other factor that affected responding in the first half of the empty portion of the probes (timing of the US-US interval) was the duration of the CS, with the shorter CS groups demonstrating more responding (less accurate timing) than the longer CS groups. It is possible that the higher level of responding in the 15-s groups was due to anticipation of the upcoming short CS. Anticipation of an upcoming trial stimulus has been demonstrated repeatedly in the peak interval timing procedure in which long unreinforced peak trials are intermixed with standard signalled fixed interval trials. Rats will typically display a gradual increase in responding near the end of the peak trial even though they never receive reinforcement at this time (e.g., Church et al., 1991). This “tail” in responding has been demonstrated to be due to anticipation of the upcoming trial stimulus (Church et al., 1991). One would expect more of an anticipatory response in the 15-s groups compared to the 60-s groups because the onset of the 15-s CS occurs later in the US-US interval and the 15-s CS was a more salient stimulus for conditioning due to its short duration.

The reason for the failure to observe a US-preexposure effect in the present design is not apparent. We have been unable to discover any published instances of US-preexposure effects in the rat appetitive-conditioning paradigm with

magazine entry as the conditioned response. Thus, one (unsatisfying) possibility is that this paradigm is insensitive to US-preexposure effects. One difference between the present paradigm and other paradigms that have revealed US-preexposure effects is that the same response is elicited by the US-US interval and the CS onset-US interval. In pigeon autoshaping, exposure to unsignalled USs results in the acquisition of goal-tracking behaviors such as head entry into the food cup. However, the keylight CS results in sign-tracking behaviors such as keypecking. Similarly, Timberlake (1986) found a US-preexposure effect with rats when the CS evoked ball bearing contact rather than goal-tracking behavior. Thus, one factor that may promote observation of the US-preexposure effect in appetitive paradigms is behavioral competition between goal-oriented and sign-oriented responses.

The preexposure regimen used in Experiment 1 involved immediate onset of preexposure treatment after the rats were placed in the experimental chambers. Goddard and Jenkins (1988) observed that their earlier attempts to produce US preexposure in pigeon autoshaping had also failed, but when they instituted a presession wait before the onset of US deliveries then the US-preexposure effect emerged. They hypothesized that the insertion of a presession wait results in the first US serving as a better predictor of the subsequent US than other cues such as entering the experimental chamber. Thus, although they did not directly assess the affect of a presession wait within a single experiment, Goddard and Jenkins (1988) hypothesized that a delayed start of US exposure treatment was necessary to produce the US-preexposure effect in pigeon autoshaping. Accordingly, a direct assessment of the effect of presession wait time on the occurrence of the US-preexposure effect was the primary focus of Experiment 2.

Experiment 2

Experiment 2 sought to explore the role of a long presession wait time prior to the first US delivery in the occurrence of the US-preexposure effect. If a long presession wait facilitates learning of the US-US interval then, following training on a fixed US-US schedule, there should be clear differences in acquisition of the US-US interval compared to a group that received only a short presession wait time before the first US delivery of a session. Any difference in US-US learning should then translate into differences in subsequent conditioning to the CS.

An additional goal of the manipulation of presession wait time was to record and analyse behavior during the presession wait and during the US delivery portion of the preexposure phase to gain further insight into possible sources of any effect of presession wait time.

In addition, Experiment 2 used a CS duration that filled most of the US-US interval in an attempt to increase the likelihood of observing a US-preexposure effect. Because the goal of Experiment 1 was to determine whether CS duration affected the magnitude of the US preexposure CS duration was increased in Experiment 2 to attempt to maximize any effect by filling most of the US-US interval with the CS. Goddard and Jenkins (1988) found that pigeons that received a 10.5 s US-US interval displayed a greater retardation in conditioning to a 10 s CS compared to a group that received a 100.5 s US-US interval and a 10-s CS, suggesting

that the degree to which the CS filled the US-US interval contributed to the difference in performance. Although there are other factors that differed between the groups such as mean US-US interval and mean US-CS interval, it is possible that filling the US-US interval with the CS enhanced the US-preexposure effect.

Finally, an extinction phase was added after the end of the conditioning phase to measure CS responding in the absence of any influence of US exposures.

Method

Subjects. Subjects were 18 male Sprague-Dawley rats (Harlan UK) aged approximately 60 days at the beginning of the experiment. Housing and maintenance procedures were the same as Experiment 1.

Apparatus. The apparatus was the same as Experiment 1.

Procedure. The 18 rats were randomly assigned to three groups (n = 6): P90S, P90L, and U90L. To examine the role of presession wait time in modulating the US-preexposure effect, groups P90S and P90L were given four sessions of US preexposure, but with different amounts of time in the box prior to the onset of the preexposure treatment.

US Preexposure (Sessions 1-4): Onset of the houselight cued the beginning of the experimental session. In the short presession wait group (P90S), 2.5 min elapsed between house light onset and the delivery of the first food US. In the long presession wait group (P90L), 31.5 min elapsed before the delivery of the first US. In total 60 US presentations were delivered. Following the delivery of the last US the house light was turned off. Rats in the control group (U90L) were placed in the chambers for 120 min with the house light on; there were no other stimuli or any reinforcers delivered during this time. Each US-preexposure session lasted either 90 min (P90S) or 120 min (P90L). A single click was emitted concurrently with US delivery to ensure that the rats detected the onset of food deliveries after the presession wait time.

CS-US Training (Sessions 5-12): Following the US-preexposure sessions all groups of rats were given eight sessions of CS-US training. CS-US training consisted of the delivery of a 90-s white noise CS that filled the interval between successive US deliveries. CS onset occurred 0.5 s after US delivery and noise offset occurred 0.5 s prior to US delivery so that there was a 1-s gap in CS delivery surrounding the time of food occurrence. A single click was issued concurrently with US delivery as in the prior phase. In total, 54 CS-US trials were delivered. A further 6 probe trials consisted of a 180-s empty duration, followed by a 90-s CS delivery. Due to a programming error, during the first 4 CS-US training sessions (sessions 5-8) a US was delivered at the end of the 180-s portion of the probe trial (just prior to CS onset), so analysis of CS performance could not be conducted. For a further four sessions (sessions 9-12) the US was delivered at the end of the following CS delivery. The probe trials were randomly intermixed with the CS-US training trials. The presession wait for groups P90S and P90L was maintained at 2.5 and 31.5 min, respectively. Group U90L received a 31.5 min presession wait prior to the onset of CS and US deliveries.

Extinction (Sessions 13-15): During the extinction phase, rats received 30 nonreinforced presentations of the 90-s CS. The rats received a presession wait period before the onset of extinction that was the same as in the prior phase. Successive CS deliveries were separated by a 90-s fixed interval that was devoid of any other stimuli or reinforcers.

Results

US Preexposure. The mean rate of responding did not change over the course of four sessions of US preexposure training, $F < 1$, and response rates were similar irrespective of the presession wait that the groups were exposed to, $F < 1$. The shape of the temporal gradients during the food-food interval was comparable to Experiment 1 (see Figure 1), and there were no differences in the shape of the gradients between the two preexposed groups.

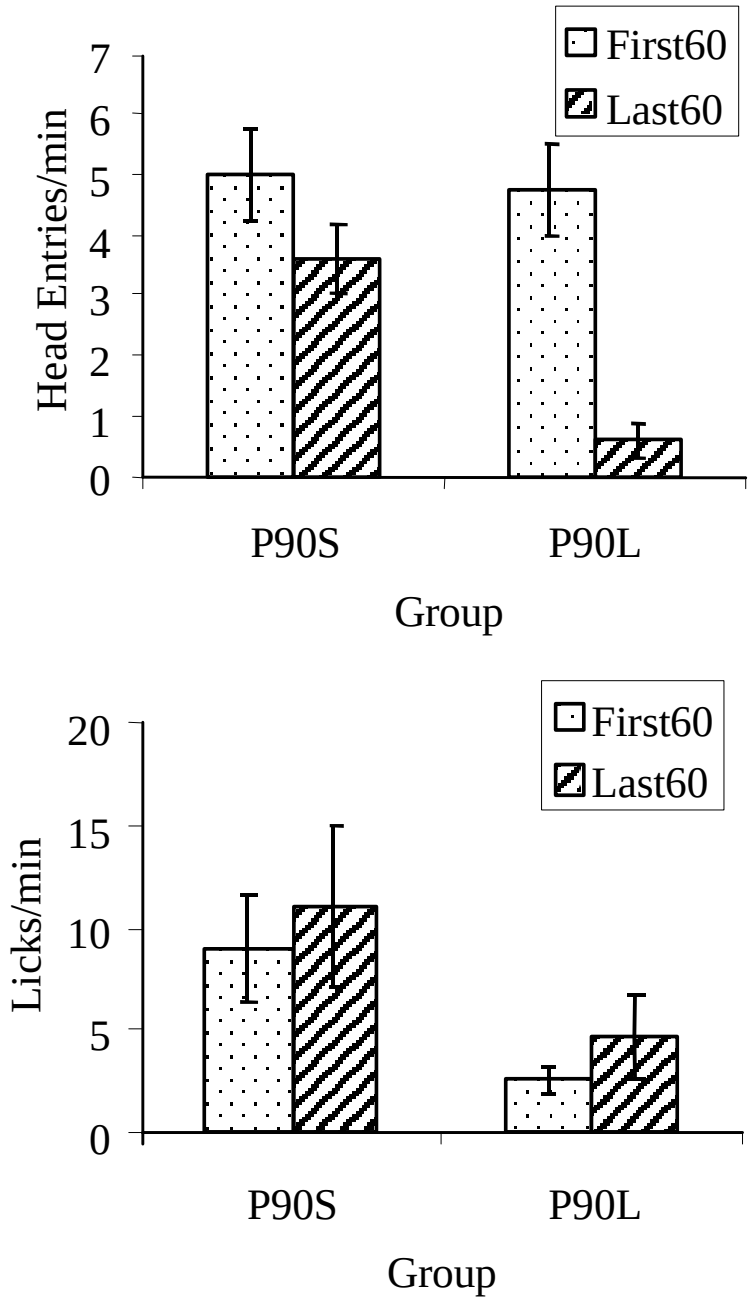

Figure 4. Top panel: Head entries per minute produced by groups P90S and P90L in the first 60 s and last 60 s of the presession wait time prior to the first US delivery of preexposure sessions in Experiment 2. Bottom panel: Licks per minute produced in the first 60 s and last 60 s of the presession wait time.

One goal of the present experiment was to examine behavior during the presession wait. Accordingly, the activity of the rats prior to the first US delivery in the US-preexposure sessions was investigated. Figure 4 displays the mean rate

of head entry (top panel) and licking (bottom panel) for the two groups during the first and last 60 s of the presession wait time. Head entry behavior was similar in the two groups at the start of the presession wait, $F < 1$, but decreased in group P90L to a near-zero level by the end of their presession wait so that the two groups differed during the last 60 s of presession wait time $F(1, 10) = 14.4$, $p < 0.01$. The rate of drinking, on the other hand, appeared to increase slightly over the presession wait. Group P90L drank less than group P90S at the start of the presession wait, $F(1, 10) = 5.8$, $p < 0.05$, but the two groups did not differ significantly at the end of the presession wait, $F(1, 10) = 2.0$. The pattern of results indicates that exploratory behavior changed over the presession wait, particularly when the presession wait was a long duration (P90L).

Finally, the rates of head entry responding during the presession wait were compared with response rates during the US-US interval (seconds 20-90) over the US exposure portion of the session with factors of group (P90S vs. P90L) and period (presession wait vs. US exposure). The response during the first 60 s of the presession wait was not different from the response rate during US exposure, $F(1, 10) = 4.7$, $p = 0.06$, there was no group effect, $F < 1$, nor any group x period interaction, $F < 1$. On the other hand, the response rates during US exposure were significantly higher than during the last 60 s of the presession wait, period main effect: $F(1, 10) = 34.5$, $p < 0.001$. There was no group main effect, $F(1, 10) = 1.1$, and group assignment did not interact with period, $F(1, 10) = 2.3$, $p = 0.16$.

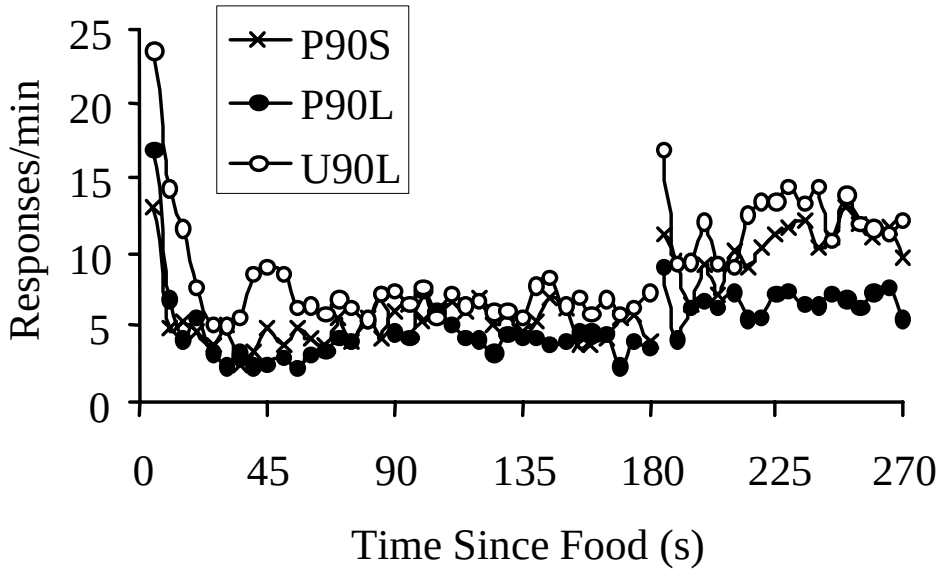

Figure 5. Response rate as a function of time since the prior food delivery during probe trials in Experiment 2. CS onset is indicated by a break in each function.

CS-US Training. The response rates produced by the three groups on the probe trials for the last four sessions of CS-US training are plotted in Figure 5 as a function of time since the prior food delivery. The time of CS onset is indicated by a break in the functions. Probe trials consisted of a 180-s empty interval followed by a 90-s CS that ended with delivery of a single food pellet. Responding was high during the start of the probe, which was probably related to consumption of the

previously delivered food US. There appeared to be a difference in response rates during the empty portion of the probe trial, with group U90L demonstrating the highest response rate. Mean response rates were calculated over the 20-90 s portion of probe trials, and these revealed a significant effect of Group, $F(2, 15) = 7.5$, $p < 0.005$. Post hoc analyses (Tukey HSD) indicated that groups P90S and P90L demonstrated lower response rates compared to group U90L.

The pre-CS rates of responding (calculated over the last 90 s of the empty portion of probes) were examined to determine whether there were any differences among the groups beyond the expected time of food delivery (at 90 s). An ANOVA revealed that there were no group differences, $F(2, 15) = 1.7$.

As seen in Figure 5, CS onset at 180 s resulted in a sudden increase in response rate in all three groups that was followed by a more gradual increase in rate over the course of the CS duration (i.e., all groups demonstrated evidence of timing of the CS duration). Responding was highest in groups P90S and U90L. To further assess differences in CS responding on the probes, elevation scores were calculated by subtracting the mean response rate during the last 90 s prior to CS onset from the mean response rate over the CS.

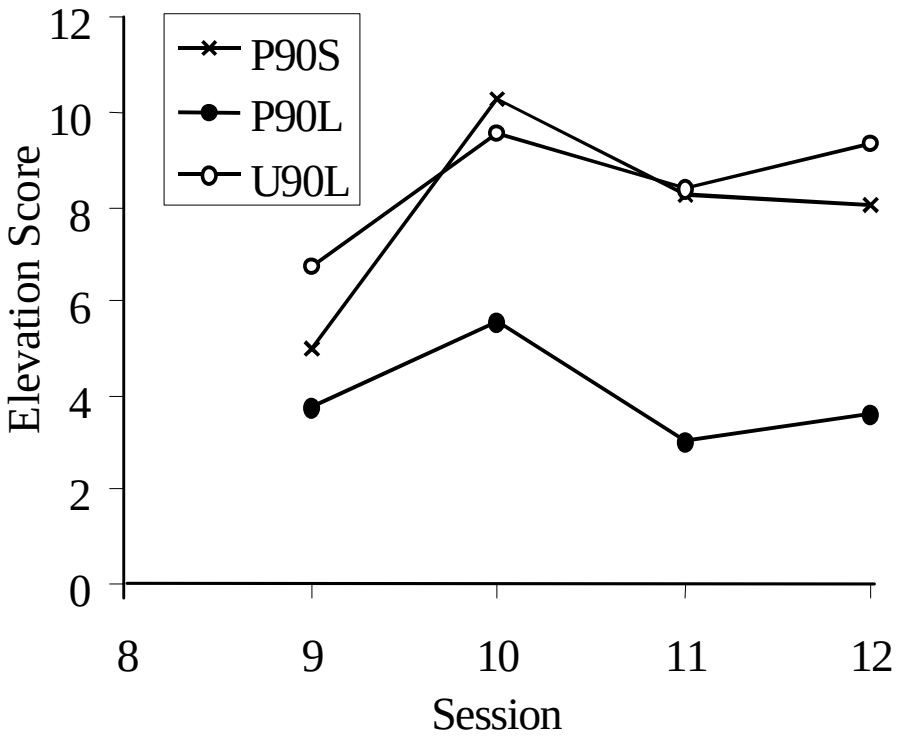

Figure 6. Elevation scores as a function of sessions of training over the last four sessions of CS-US training in Experiment 2.

The elevation scores during probe trials in the CS-US training phase are shown in Figure 6 over the course of the last four sessions of CS-US training. Elevation scores did not change significantly over the last four sessions of training, $F(3, 45) = 2.4$, and there was no difference between groups either as a main effect, $F(2, 15) = 1.7$, or as an interaction with sessions, $F < 1$. (The failure to observe an

effect of sessions was likely because the analysis was conducted on the last four sessions only due to a computer error during the first four sessions, by which point elevation scores were reaching asymptote.) One possible reason for the failure to observe a US-preexposure effect in the original ANOVA is that group P90S exhibited substantially more variance between rats compared to the other two groups. There were two rats in the group that produced a pattern of responding more consistent with group P90L and four rats that appeared more like group U90L. Given that there were apriori expectations of a US-preexposure effect with the long presession wait, a further analysis was conducted comparing groups P90L and U90L. Because there was no session effect in the prior analysis, the data were averaged across the four sessions. The follow-up ANOVA revealed a significant effect of group, $F(1, 10) = 7.5$, $p < 0.05$, indicating that group P90L responded less during the probe CS than group U90L.

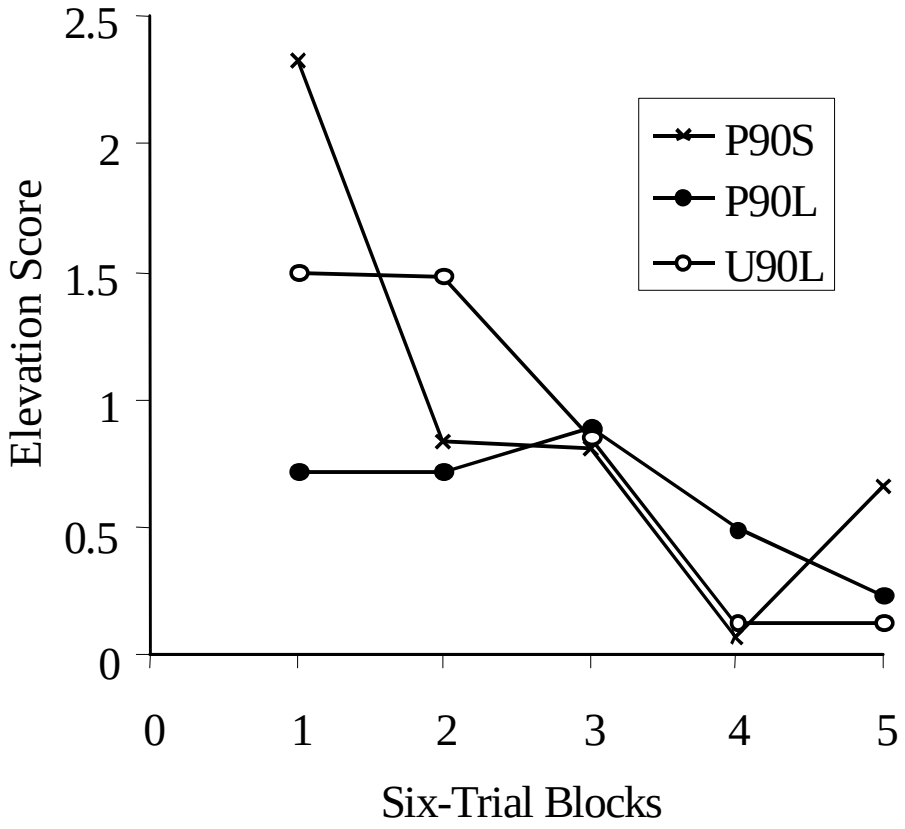

Figure 7. Elevation scores as a function of six-trial blocks of extinction over the first extinction session in Experiment 2.

Extinction. Figure 7 displays the elevation scores (CS rate – pre-CS rate) over the first session of extinction in six-trial blocks. Elevation scores during the CS revealed a similar pattern to what was seen in the probe trials during CS-US training, with the P90S and U90L groups demonstrating more responding than group P90L. Because the groups had converged by the third block of extinction, an ANOVA was conducted on the elevation scores and on the rate of responding dur-

ing the CS averaged across the first two blocks only. (CS rates were analyzed as well as elevation scores because it was noted that pre-CS rates extinguished more quickly than CS rates in some rats and this added variability to the elevation scores). The analysis of both elevation scores and CS rates, Fs(2, 15) $\leq$ 2.4, failed to reveal a group effect on CS responding. However, as in the probe trial analysis, there was substantial variance among the rats in group P90S that created homogeneity of variance problems for the ANOVA. Therefore, an additional analysis was conducted on the scores for groups P90L and U90L to determine whether there was a US-preexposure effect with the long presession wait. This analysis revealed an effect of group on the CS rates, $F(1, 10) = 7.6$, $p < 0.05$, while the group effect on the elevation scores only approached significance, $F(1, 10) = 2.5$.

Discussion

As in Experiment 1, the rats demonstrated temporal conditioning in the initial US exposure phase. The preexposed groups appeared to time the US-US interval more accurately, as evidenced by differences in the first 90 s of the probe trials between the preexposed and unexposed groups. This would be expected because the preexposed groups had received more training with the US-US interval.

Most importantly, it was discovered that a long presession wait time before the onset of US deliveries (and also a CS that filled most of the US-US interval) retarded responding to the CS (Figures 5 and 6). Direct comparison of groups with short and long presession wait times have not been previously undertaken, so the present study represents a novel addition to the understanding of factors that affect learning during US preexposure experiments. Previous between-experiment comparisons in pigeon autoshaping have also suggested that US preexposure may not occur in the absence of a long presession wait (Jenkins et al., 1981) but certainly does occur with a presession wait time of 14.7 min (Goddard & Jenkins, 1988).

Because the presession wait was maintained during conditioning at the same duration as in preexposure, it is possible that the differences in conditioning were due to an effect of presession wait in the conditioning phase rather than in the preexposure phase. However, the control group (U90L) was given a long presession wait during conditioning. If the retardation in conditioning was due to a long presession wait during the conditioning phase (instead of preexposure), then one would expect the control group to reveal similar levels of responding compared to group P90L, but instead the control group was similar to group P90S. This suggests that the effects were due to the presession wait during the US-preexposure phase (although the inclusion of a U90S control would strengthen this proposition).

An examination of behavior during the presession wait in the preexposure phase indicated that there were differences between the two preexposed groups during the preexposure phase, further suggesting that the presession wait effects were operating during US preexposure. There was a significant decline in food cup behavior between the start and end of the wait period in the P90L group compared with food cup behavior during a short wait period, group P90S. The long presession wait before initial US delivery, therefore, facilitated a reduction of exploratory behaviour by group P90L prior to initial US delivery.

The pattern of head entry for group P90L suggests that rats may have altered their search mode between placement in the experimental chamber where behaviour is expected to be focussed on potential food sources, to a state of quiescence following exploration of the chamber (see Timberlake, 2001). Group P90S would not be expected to reach a stage of quiescence since there was not enough time but might still display more generalized search behavior away from the food cup as indicated by greater drinking behavior. As such they might be expected to differ in response rate at the onset of US delivery. At US onset, group P90L demonstrated a substantial increase in head entry behavior consistent with a reinstatement of a focal search mode, group P90S demonstrated a less pronounced (but still significant) increase in food cup behavior indicating that the two groups were in different search modes. These results support the notion that group P90L was in a quiescence mode whereas group P90S was in a general mode (Timberlake, 2001). During the US exposure period, response rates increased to comparable levels as were observed during the first 60 s of the presession wait. However, there was no difference between groups in mean response rates or in the shape of the temporal gradients during the US-US interval; if the phase of search mode at the time of onset of US exposure affected learning about US deliveries, then one would expect a difference in responding during the US-US interval.

Goddard and Jenkins (1988) proposed that a long presession wait would cause the first US to be a better predictor of the next US than any other cues (such as placement in the experimental chambers), thereby increasing the efficacy of US-US signalling. It is possible that US-US signalling is more effective if exploratory behaviors are allowed to wane in frequency.

An alternative possibility is that the presession wait time may allow for a dissipation of posthandling anxiety. A long presession wait has been found to facilitate delay conditioning in pigeon autoshaping (e.g. Papini, Linwick & Overmier, 1987). Papini et al. (1987) found that a presession wait time of 300 or 3000 s resulted in a facilitation of the acquisition of keypecking in a standard autoshaping design, in comparison to a 30 s presession wait. Thus, the effects of presession wait may be on stimulus processing in general, rather than specifically on US-US signalling.

It does appear that US-preexposure effects occur in the rat goal-tracking paradigm when the CS fills most of the US-US interval. During the probe trials in which timing from the US and CS onset events was uncoupled, there was evidence of temporal control by both cues. Responding increased gradually during the first 90 s of the probe trial, reaching a peak near the expected time of US delivery; this pattern is indicative of timing of the US-US interval. Following CS onset on probe trials, responding increased gradually throughout the CS duration, indicating that the rats in all groups had learned to time the duration of the CS. However, the magnitude of conditioned responding during the CS was impaired in group P90L.

Experiment 3

The present experiment examined the effect of CS duration on the US-preexposure effect. Experiment 2 indicated that US preexposure is observed when the CS fills most (89 of 90 s) of the US-US interval. It is possible that the US-preexposure effect might only be observed under these conditions. Alternatively, the effect of CS duration might be graded, as suggested by Gallistel and Gibbon

(2000), or the effect may be insensitive to CS duration as suggested by context blocking (Baker et al., 1981; Hinson, 1982; Tomie 1976a, 1976b) and time of arrival (Goddard & Jenkins, 1988) accounts.

Method

Subjects. Thirty six male Sprague Dawley rats (Harlan, UK) were housed in pairs in a colony room on a 12:12 h light:dark cycle. All other details of husbandry were the same as reported in Experiment 1.

Apparatus. The apparatus was the same as in Experiment 1.

Procedure. The rats were randomly assigned to one of six groups P90, U90, P60, U60, P15 and U15. There were three phases to the experiment, a US preexposure phase, a CS-US training phase and extinction.

US Preexposure (Sessions 1-6): Overall, conditions were similar to those of Experiment 2. The rats were placed in the experimental chambers with the house lights switched on. Groups P90, P60 and P15 were presented with unsignalled food deliveries on a fixed interval of 90 s and a single click was delivered concurrently with food delivery as in Experiment 2. In total, there were 60 food deliveries during each of 6 daily sessions. The three groups, U90, U60 and U15 were placed in the experimental chambers for a similar duration to the preexposed groups but did not receive any food deliveries. Food delivery commenced 30 min after rats were placed in the experimental chamber and sessions lasted for 2 hrs.

CS-US training (Sessions 7-16): Following US preexposure, 10 CS-US sessions were conducted. All six groups received 60 CS-US presentations per session with a fixed 90-s interval between US deliveries; there was a 30-min presession wait before the onset of CS-US deliveries. Groups P90 and U90 received a 70 dB white noise CS that filled all but 1 s of the US-US interval. CS offset occurred 0.5 s prior to US delivery, and CS onset occurred 0.5 s after US delivery. Groups P60 and U60 received a 60 s tone and CS offset was contiguous with US delivery. Groups P15 and U15 received a 15 s tone with CS offset contiguous with US delivery. On a random 6 trials (10%) during each 60-trial session, probes were delivered. These consisted of a 180-s empty period before CS onset, with the CS lasting for the usual duration and ending with food delivery. Session durations were approximately 2 h for each group.

Extinction (Sessions 17-20): During extinction, rats received 30 nonreinforced CS presentations; there was a 30-min presession wait before the onset of CS presentations. The CS duration was the same duration presented during CS-US training. There was a 90-s interval that separated each CS; this interval was devoid of any stimuli or reinforcers.

Results

US Preexposure. There was an increase in the rate of responding as defined by head entry to the food cup over the six sessions of US preexposure, $F(5, 75) = 12.8$, $p < 0.001$, but the rate of responding between the three preexposure groups did not differ, $F < 1$. As in the prior experiments (see Figure 1), all three preexposed groups learned to time the food-food interval and the pattern of responding was similar in all three groups.

CS-US Training. The response rate as a function of time since food during probe trials is shown in Figure 8. The time of CS onset is indicated by a break in the functions at 180 s. Response rates during the empty portion of the probe were initially high, then decreased, and then increased gradually up until 90 s (the time when food delivery would normally occur). An ANOVA conducted on response rates from 20-90 s of probe trials revealed no difference based on CS duration, $F(2, 30) = 1.0$, and no interaction between groups based on CS duration and US preex-

posure, $F(2, 30) = 1.2$. There was a difference between groups based on preexposure, $F(1, 30) = 9.3$, $p < 0.01$, in that more responding was evidenced by groups that did not experience US preexposure. Thereafter, responding remained relatively constant at a rate of around 5 responses/min.

However, rates of responding during the pre-CS period (the period just prior to CS onset that was equal in duration to the CS) indicated that there was no difference between groups as an effect of CS duration, $F(2, 29) = 2.0$, preexposure, $F < 1$, or the interaction between CS duration and preexposure, $F < 1$.

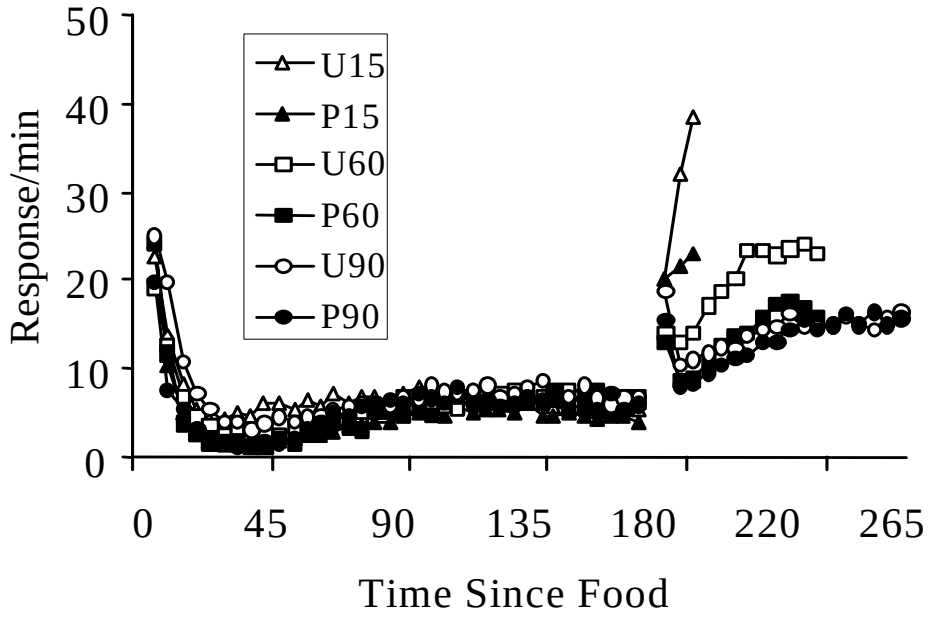

Figure 8. Response rate as a function of time since the prior food delivery during probe trials in Experiment 3. CS onset is indicated by a break in each function.

Following CS onset, there was a sudden increase in response rate, followed by a more gradual increase with response rates reaching a maximum near the end of the CS duration. The slope of increase in response rate was greater for groups that received shorter CS durations. It also appeared that the CS response was greater in (at least some) unexposed groups compared to preexposed groups with the same CS duration.

To further assess differences in CS responding, elevation scores were calculated by subtracting the mean response rate in the pre-CS period of the probe trials from the mean response rate during the CS. The duration of the pre-CS window was matched with the duration of the CS, and pre-CS responding was calculated during the period just before CS onset. The elevation scores are shown in Figure 9, as a function of sessions of training. The elevation scores were higher for groups with shorter CSs, and for groups that did not receive the US-preexposure treatment.

An ANOVA conducted on the elevation scores revealed an increase over sessions of training, $F(8, 240) = 12.6$, $p < 0.001$, and that elevation scores were higher when CS duration was shorter, $F(2, 30) = 10.1$, $p < 0.001$. Analysis of the preexposure effect was conducted for each pair of groups (experimental vs. con-

trol) that received a given CS duration. These contrasts revealed a trend toward a preexposure effect, but none of the comparisons were statistically significant, 90 s, $F(1, 10) = 3.4$, $p = 0.10$; 60 s, $F(1, 10) = 4.3$, $p = 0.06$; 15 s, $F(1, 10) = 4.4$, $p = 0.06$.

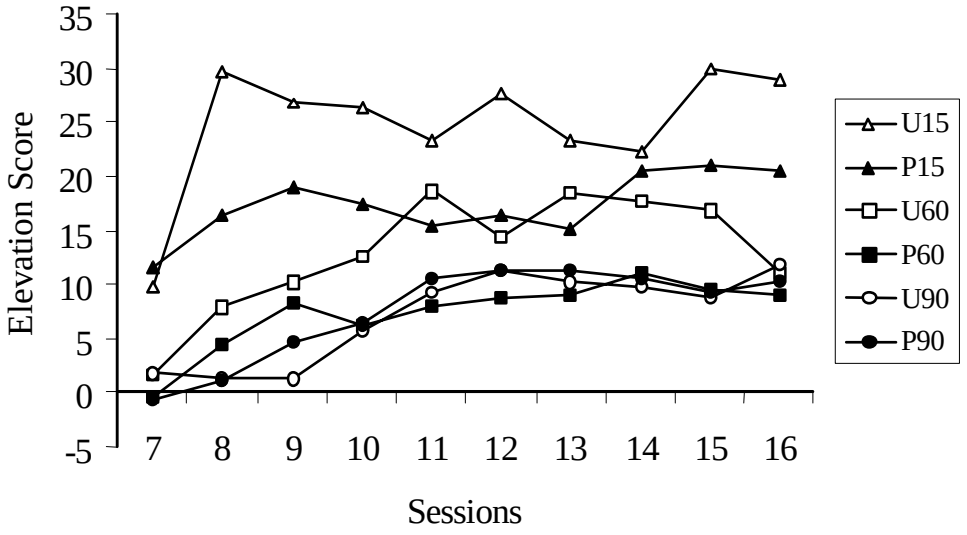

Figure 9. Elevation scores as a function of sessions of CS-US training in Experiment 3.

Extinction. Responding during extinction is displayed in Figure 10 as a function of sessions. The groups had partially converged by the second session and fully converged by the third session of extinction. As in the compound phase, there was a clear effect of interval duration on responding and there also appeared to be a preexposure effect. An ANOVA was conducted on elevation scores as well as mean rates of responding during the CS over the first session of extinction, where differences among groups were most pronounced. There was an effect of interval duration on both the elevation scores, $F(2, 30) = 10.9$, $p < 0.001$, and CS rates, $F(2, 30) = 10.9$, $p < 0.001$, but the preexposure effect did not reach statistical significance on either measure: CS rates, $F(1, 30) = 1.3$; elevation scores, $F(1, 30) = 1.3$; and there was no interaction of preexposure with duration: CS rates, $F < 1$, elevation scores, $F < 1$. Further analyses were conducted on pairs of groups to determine whether there was a preexposure effect for some subset of the intervals. These analyses revealed a significant preexposure effect for the groups that received 90-s CS durations and this effect was apparent in both the elevation scores, $F(1, 10) = 10.0$, $p < 0.01$, and CS rates, $F(1, 10) = 6.2$, $p < 0.05$. There was also evidence of a preexposure effect with a 60-s CS in the elevation scores, $F(1, 10) = 6.3$, $p < 0.05$, although the CS rates did not differ between the preexposure and unexposed groups, $F < 1$. However, there was no evidence of a preexposure effect in the groups that received 15-s CS durations on either measure of behavior, Fs < 1.

Discussion

In Experiment 3, all experimental groups received a presession wait time of 30 min before experiencing US-preexposure treatment. A US-preexposure effect was observed if the CS filled all (90 s) or most (60 s) of the US-US interval, but not when the CS was very short (15 s). Thus, the magnitude of preexposure was affected by CS duration. The results suggest that CS onset-US interval duration affects preexposure in a graded fashion.

The pattern of results is generally consistent with RET (Gallistel & Gibbon, 2000), which predicts that CS duration should interact with US-preexposure treatment in the present design to produce an increasing impact of US preexposure as CS duration is lengthened. The results suggest that some sort of interval comparison mechanism may be warranted.

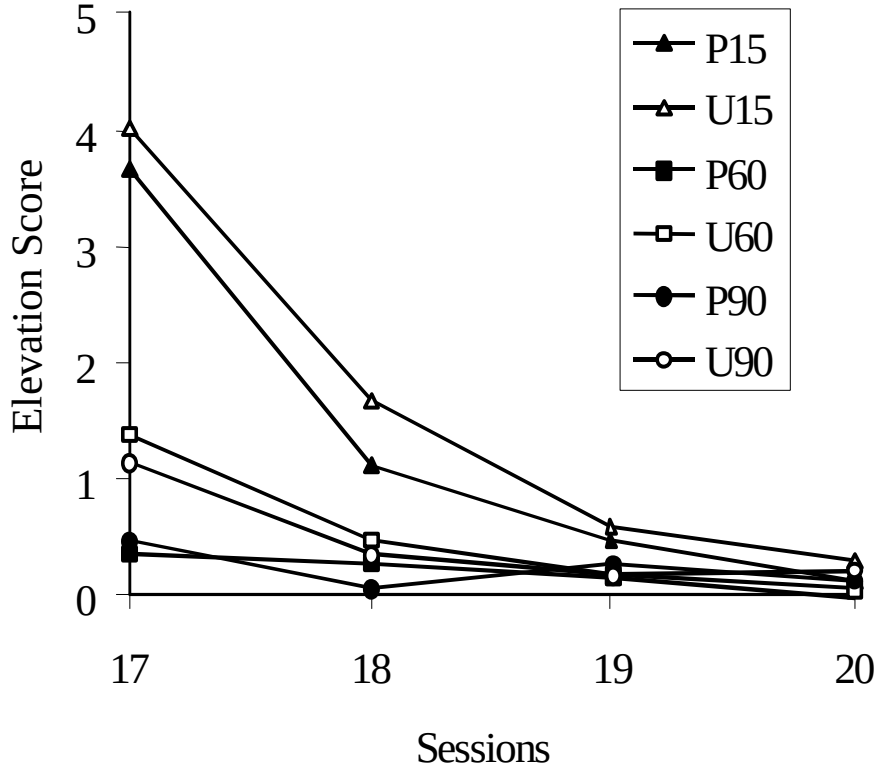

Figure 10. Elevation scores as a function of sessions of extinction in Experiment 3.

General Discussion

During the empty portion of probes in all three experiments, rats demonstrated an increasing response rate that reached a maximum at 90 s, the expected time of US delivery relative to the prior US delivery. Following CS onset, response rates increased as a function of time since CS onset reaching a maximum at the end of the CS (the expected time of US delivery relative to CS onset). The slope of increase in response rate during the CS was related to CS duration, with shorter CSs resulting in steeper response functions. The pattern of responding on the probes

suggests that the rats timed the US-US and CS onset-US intervals independently. On CS-US trials, both the prior US and CS onset predict the upcoming US arrival at the same moment. It is possible that the rats could treat the two cues as an integrated serial compound, but this would lead to an interference of timing behavior when the two cues are uncoupled in the probe trials. Instead, the present results are consistent with other reports of independent, simultaneous timing from two time markers in basic operant and classical conditioning procedures (e.g., Desmond & Moore, 1991; Kirkpatrick & Church, 2000b; Meck & Church, 1984).

The central finding of the present study is that CS duration modulated the magnitude of the US-preexposure effect, and this effect appeared to be graded as US preexposure was strongest with a CS duration of 90 s, moderate with a CS duration of 60 s, and not apparent with a CS duration of 15 s (Figures 9 and 10).

Speculation about why preexposure to USs results in subsequent decrements in conditioning includes context blocking, habituation, and learned laziness. (See Goddard & Jenkins, 1988 for a review of various accounts and their relevance to predicting the role of temporal variables.) None of these directly postulate any effect of CS duration on the magnitude of the US-preexposure effect.

It is known that CS duration directly affects the magnitude of conditioned responding (e.g, Gibbon et al., 1977; Gibbon & Balsam, 1981; Kirkpatrick & Church, 2000b); likewise the attenuating effect of US preexposure is also well established (e.g., Braveman, 1975; Dickinson, Hall, & Mackintosh, 1976; Durlach, McQuoid & Regehr, 1990; Gillan & Domjan, 1977; Goddard & Jenkins, 1988; Hinson, 1982; Mowrer, 1987). It is possible that the present results could be explained by a sort of summation of independent effects of CS duration and US preexposure. Although pure summation would lead to the prediction of a preexposure effect at both long and short CS durations, it is possible that the US-preexposure effect is only observed if parameters that yield weak conditioning are employed. One parameter that is known to weaken conditioning is lengthening the CS duration, as seen in the present studies. Thus, the interaction between CS duration and US-preexposure treatment could be modelled using a context blocking account by presuming that the CS salience is reduced for longer duration CSs, thereby yielding a more robust effect of US-preexposure treatment. Although this approach may explain the present results, it does not apply readily to explaining the role of the mean and variability of the US-US interval in modulating the US-preexposure effect. It would be preferable if a single theoretical framework could explain all established effects of temporal variables in the US-preexposure paradigm.

Although the time-of-arrival hypothesis has successfully accounted for the effects of mean and variance of the US-US interval and interval shifts in the US-preexposure effect, it predicts no effect of CS duration on the magnitude of the US-preexposure effect if the US-US interval is held constant (both across phases and across groups). The present results do not support this account. It appears instead that a mechanism that compares the US-US and CS onset-US intervals may be needed to explain the results.

Gallistel and Gibbon's (2000) rate expectancy theory does predict an effect of CS duration on US preexposure, with shorter CSs demonstrating less retardation in conditioning. However, the fact that any learning was observed in the 90-s groups (even the control group) is inconsistent with RET. In the 90-s condition the CS filled 89 s of the 90-s US-US interval, producing an exceptionally small I/T

ratio (1/89). It should take many thousands of trials for the rats to learn this task, but in Experiments 2 and 3 the rats demonstrated an increase in conditioned responding after only one session (60 trials) and reached asymptotic levels within 200-300 trials. In addition, although RET provides a reasonably good explanation of the current pattern of results, it does not account for the effects of variability in the US-US interval or shifts in the mean US-US interval between preexposure and CS-US training phases. Therefore, an alternative account appears to be needed.

One possible approach to explaining the effects of temporal variables on US preexposure is the conditional expected time function, which has been implemented for simulation as Packet Theory (Kirkpatrick, 2002; Kirkpatrick & Church, 2003). The conditional expected time function is the expected time remaining in an interval until US delivery as a function of time since the onset of the interval. For the fixed intervals used in the present study, the conditional expected time function at interval onset is equal to the duration of the fixed interval and decreases toward zero by 1 s during each second of the interval duration, but for an exponential random interval the conditional expected time remains constant at the mean of the random interval.

Although Packet Theory has not yet been extended to deal with cue competition effects, it is possible that comparison of the conditional expected time functions may prove effective in predicting the various interval effects on US preexposure. Figure 11 demonstrates the effect of different interval manipulations on the conditional expected time function. In the left column are the relevant expectations for the US-US (solid lines) and CS onset-US (dashed lines) intervals used in Experiment 3. There are two main points in time where differences in the expected time are most likely have an impact on behavior, the initial expectation (E_0) and the final expectation at the time of US delivery (E_*). The initial expectation is equal to the mean interval duration regardless of interval type. The value of the final expectation will depend on the distribution of interval durations. In a fixed interval the final expectation will be zero, but adding variability will affect the final expectation.

The manipulation of CS duration in the present experiments has a profound effect on the relationship of the US-US and CS onset-US conditional expected time functions. When the CS fills the entire interval (top left panel of Figure 11) the two expectations overlap entirely, but if CS duration is shortened, then the expected time functions only partially overlap. One major difference in the expectations here is in the initial expectation; the final expectation is the same. When the CS duration is 60 s, the initial expectations of the US-US and CS onset-US intervals differ by 30 s (or a ratio of 90/60 = 1.5) and when the CS duration is 15 s the initial expectations differ by 75 s (or a ratio of 90/15 = 6). It is possible that the US-preexposure effect is determined, at least in part, by the comparison of the US-US and CS onset-US expectation functions. If the US expectation is already a good predictor of the upcoming US, and CS onset does not add significant new information, then a retardation in conditioning to the CS is expected to occur. The present results indicate that differences in the initial expectations may be an important determinant of the magnitude of the US-preexposure effect. However, from the present studies it cannot be determined whether the absolute difference or the ratio of the two intervals is the key factor.

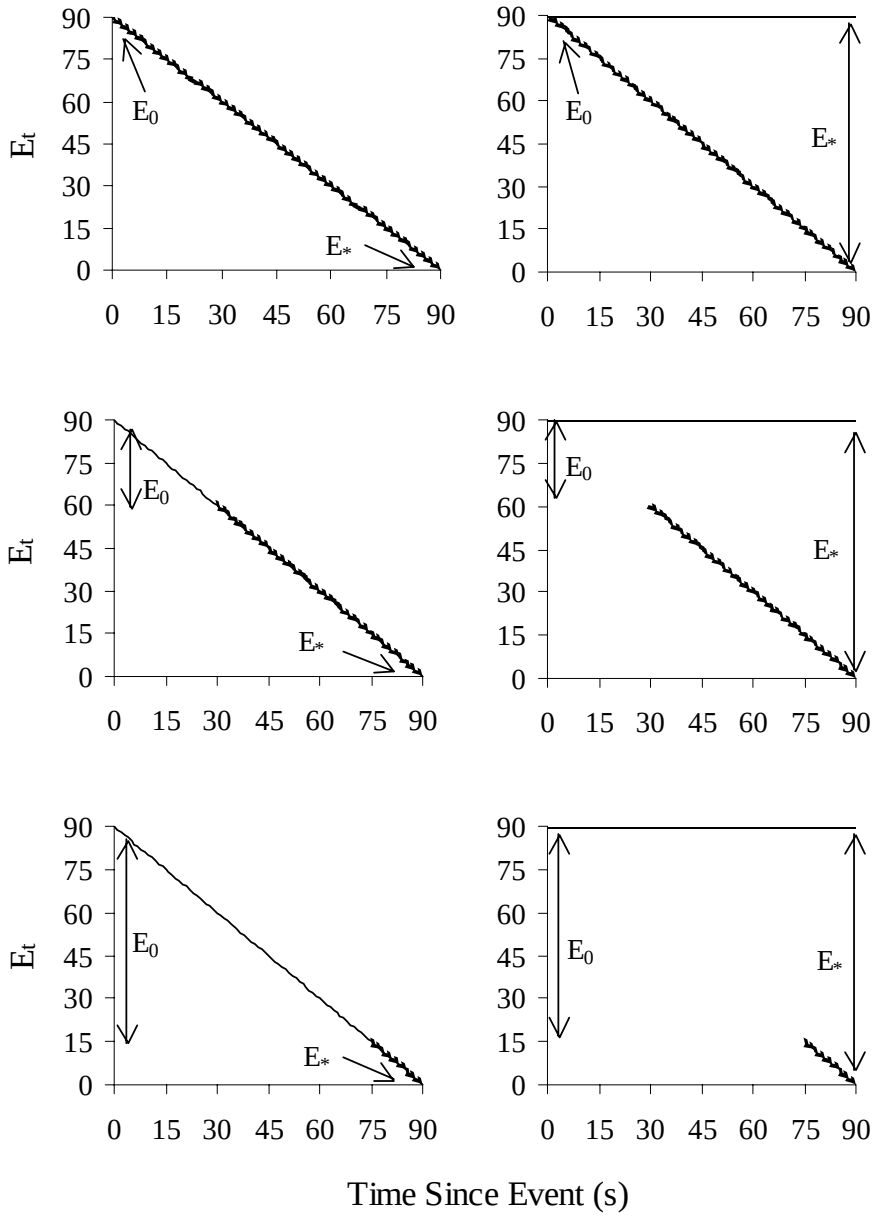

Figure 11. Conditional expected time to food as a function of time since event (prior US or CS onset) for different pairs of US-US (solid lines) and CS onset-US (dashed lines) intervals. Fixed intervals produce linearly decreasing expected time functions (left column). The left column of the figure displays the expected time functions for a fixed 90-s US-US interval with different CS onset-US intervals of 90 s, 60 s, and 15 s from top to bottom. The right column of the figure displays the expected time functions for a random 90-s US-US interval with different fixed CS onset-US intervals of 90 s, 60 s, and 15 s from top to bottom. There are two key points where differences in expectations may be assessed, the initial value (E_0) and the value at the time of US delivery (E_*).

The conditional expected time function may also explain the other reported effects of temporal variables on US preexposure. The effect of mean US-US interval on US preexposure would emerge from the same factors as the effect of CS duration. If CS duration is held constant, then manipulation of the US-US interval

will change the degree of overlap in the two expectations and thus would affect comparisons of the initial expectation. The right column of Figure 11 demonstrates the effect of variability in the US-US interval on the resulting conditional expected time functions. An exponential random 90-s US-US interval has a conditional expected time function that remains constant at the mean (90 s). When this expected time function is now compared to the fixed 90, 60, and 15 s CS onset-US interval expectations it can be seen that there are substantial differences in the final expectation (which is 90 s for the US-US interval in all three examples) as well as the initial expectations. Thus, it is possible that the reason why variable intervals produce a weaker or non-existent US-preexposure effect may be due to the contribution of a comparison of the final expectations. In the examples in Figure 11, the fixed duration CS is a better predictor of the upcoming US (even when the mean duration is the same–top right panel) because it has a shorter final expectation. Finally, shifting the US-US interval between preexposure and CS-US training phases would be expected to alleviate US preexposure because the previously established US-US expectation would no longer be relevant and therefore would not influence responding to the CS.

In summary, the present set of experiments implicated the role of CS duration in modulating the US-preexposure effect and these results join a host of other effects of temporal variables on the magnitude of US preexposure. It is apparent that temporal variables contribute importantly to US preexposure, as well as other cue competition phenomena (e.g., Savastano & Miller, 1998). The present results demonstrate the importance of CS duration as well as the US-US interval in determining US preexposure and thus represent a novel and potentially important addition to the understanding of temporal variables in conditioning. The results also suggest that some sort of interval comparison may be a productive means of explaining the results. The rats learned the duration of both the US-US and CS onset-US intervals in the present study, an important prerequisite to interval comparison. Moreover, it is known that animals are capable of judging relative interval durations (Fetterman & Dreyfus, 1986, 1987) and thus would presumably be able to make the sort of comparisons that are proposed here. However, further research will be needed to determine the critical features of the interval comparison process.

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