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Relative temporal representations in Pavlovian conditioning

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Abstract

The transfer of relative temporal representations was assessed in a series of three experiments. In each experiment, rats (*Rattus norvegicus*) received one set of conditioned stimulus (CS) and intertrial interval (ITI) durations in Phase 1 and another set in Phase 2. The ratio between the CS and ITI intervals was either changed or maintained across phases. On the hypothesis that relative temporal representations are learned, groups receiving maintained temporal ratios across phases were expected to display greater change in responding upon encountering the new intervals. When the CS duration decreased across phases, maintaining the temporal ratio did lead to greater change in Day 1 of Phase 2 towards the final pattern of responding. However, when the CS increased across phases, maintaining the temporal ratio across phases did not facilitate adjustment to the new intervals, suggesting that extinction of previously reinforced times induced new learning. These results provide evidence that under some conditions, relative relationships in temporal maps may survive transformation-of-scale, like relative relationships in spatial maps.

Keywords

interval; map; rat; representation; temporal; transfer

1. Introduction

In Pavlovian delay conditioning, there is an increased likelihood of a conditioned response (CR) during the CS as the time of the unconditioned stimulus (US) approaches. Animals learn that the CS signals the delivery of the US, in addition to learning the approximate time of US delivery (Balsam and Gallistel 2009; Drew et al. 2005; Pavlov 1927). It has been suggested that during Pavlovian conditioning, animals encode the temporal relationships between these events in temporal maps (Arcediano, Escobar, and Miller 2005; Balsam and Gallistel 2009; Honig 1981).

Temporal maps may share properties with spatial maps, such as integration of separate maps via common elements. The integrative feature of temporal maps was successfully demonstrated by Arcediano, Escobar, and Miller (2003) and Arcediano et al. (2005). In their experiments, subjects integrated one map indicating the association US→S1 with a second map containing

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the association $S2 \rightarrow S1$. By using the $S1$ element found in both maps, subjects formed a new association between $S2$ and US .

This integrative property has also been demonstrated in spatial maps. For example, spatial maps of large areas are acquired by integrating information across experiences (Collett, Harland, and Collett 2002; Gallistel and King 2009; O'Keefe and Nadel 1978; Shapiro, Tanila, and Eichenbaum 1997). In addition, Blaisdell and Cook (2005) showed that pigeons were able to integrate two separately learned spatial relationships, one between landmarks $L1$ and $L2$ and the other between $L2$ and a hidden food goal. The pigeons inferred the location of the hidden food goal when presented with $L1$ alone, demonstrating the successful combination of the two spatial relationships, using $L2$ as the integrative element.

There may be other similarities between spatial and temporal maps. For example, information in a spatial map is encoded in the relative relationships between landmarks, resulting in "transformation-of-scale," whereby relative relationships within a map are maintained regardless of the map's size. Whether a map has been shrunk to the size of a postage stamp or has been enlarged to the size of a billboard, it can still be effectively used for navigation, since the relative relationships contained within the map are preserved. It appears that animals can use transformation-of-scale in spatial maps to find new locations. Clark's nutcrackers, for example, can use relative geometric relationships between landmarks to find hidden food and can transfer these relationships to new interlandmark distances (Jones et al. 2002; Jones and Kamil 2001; Kamil and Jones 2000; Spetch et al. 2003). For example, the nutcrackers learned to find food that was hidden halfway between two landmarks even when they had not been previously trained on the particular absolute distance between the landmarks (Kamil and Jones 2000). The ability to transfer acquired information about relative spatial relationships to new distances means that the nutcrackers do not have to approach each distance as a brand-new learning experience.

Do relative representations also guide behavior in the temporal domain? It is possible that animals may use relative relationships between intervals in temporal maps in the way that they use relationships between landmarks in spatial maps. There is some evidence consistent with this idea. Fetterman, Dreyfus, and Stubbs (1989, 1993) found that pigeons are sensitive to relationships between intervals. The pigeons received a red light and a green light of various durations (T_1 , T_2). They were then presented with a two-alternative, forced-choice procedure: One response was reinforced if the ratio of the light durations ($T_1:T_2$) was greater than a criterion ratio, and the other response was reinforced if the ratio was less than the criterion ratio. Surprisingly, the pigeons were as successful as humans in this relational temporal task. Molet and Zentall (2008) and Zentall, Weaver, and Clement (2004) also demonstrated that animals make relative judgments about the durations of stimuli. Pigeons and humans were trained on temporal discrimination tasks and then presented with durations at the geometric mean of the acquired durations. The durations at the mean should have produced indifferent choices, but were in fact grouped with the shorter or longer alternative based on whether they had been presented as the shorter or longer choice in a separate discrimination.

Further evidence consistent with the hypothesis that animals form both absolute and relative temporal representations comes from analyses of acquisition in Pavlovian conditioning. Animals show patterns of responding that indicate they have knowledge of the absolute duration of a CS (Balsam, Drew, and Yang 2002; Drew et al. 2005). However, acquisition speed, at least in some cases, depends on the duration of a CS relative to the duration of the time between trials (Balsam and Gallistel 2009; Gallistel and Gibbon 2000; Gibbon and Balsam 1981). In explaining these results, it was assumed that animals learned the absolute durations of events and then compared them (Balsam, Fairhurst, and Gallistel 2006; Balsam and Gallistel

2009; Gibbon and Balsam 1981). However, it is also possible that a relative representation is formed that directly captures the relationship between intervals and controls acquisition speed.

In the current study, we explored the idea that animals encode the relative relationships between intervals in Pavlovian conditioning. Specifically, we hypothesized that if animals use relative temporal representations, preserving the relative relationship between intervals will facilitate behavioral adjustment to new intervals. In Pavlovian conditioning, previous exposure to CSs, USs, or both strongly influences subsequent performance. This path dependence is observed if subjects are initially exposed to unsignaled USs or randomly presented CSs and USs prior to CS-US pairing. Not only is subsequent learning of a CS-US relationship slower, but asymptotic performance is also changed (Baker, Murphy, and Mehta 2003; Balsam and Schwartz 1981; Claflin and Buffington 2006; Tomie 1976). Similarly, the exact parameters under which a CS-US association is acquired influence performance to the same CS and US when conditioning parameters are subsequently changed (Brown-Su et al. 1986; Lucas, Deich, and Wasserman 1981). Consequently, we would expect that subjects would be slow to change their behavior or display less change if they are switched from one set of conditioning parameters to new ones than if they are switched between equivalent conditions. We employed this strategy to investigate whether relative representations of time were acquired during Pavlovian conditioning.

In three experiments, rats were presented with one set of intervals (CS and ITI) in Phase 1 and a new set of intervals in Phase 2. Across phases, the relative temporal relationship, or ratio, between the CS and ITI interval durations was either maintained or changed. If the rats transfer their knowledge of the relative temporal relationship acquired in Phase 1 to the new intervals in Phase 2, then a maintained ratio should facilitate this transfer. While all animals are expected to change their behavior in response to the new absolute intervals, those receiving a maintained ratio in Phase 2 should display greater change more rapidly than those receiving an altered ratio. In other words, when the groups are compared at the same point in the transfer phase, those receiving the maintained ratio should show greater adjustment away from the previously acquired pattern and towards a new pattern of responding. Alternatively, if only absolute durations, rather than relative temporal relationships, are learned, there should be no advantage to preserving the ratio between the CS and ITI in the transfer test.

2. Experiment 1

Experiment 1 was conducted to determine if rats would transfer the relative temporal relationship between an acquired CS and ITI to new intervals. All rats received a CS of 12s in Phase 1 and a CS of 24s in Phase 2, but the ITI durations were varied so that one group received a maintained temporal ratio in Phase 2, while the other group received a changed ratio.

2.1. Materials and methods

2.1.1. Subjects—Subjects were 16 male Sprague-Dawley rats from the Charles River laboratories. They were housed in pairs in Plexiglas cages and kept on a 12-hour light-dark cycle. They were given free access to food for one hour after each session and had continuous access to water. The rats were used in prior operant conditioning experiments unrelated to the current topic.

2.1.2. Apparatus—Eight Med Associates conditioning chambers were used. Each chamber measured 30 × 24 × 21 cm. The front and back walls and ceiling of the chamber were Plexiglas, and the sides were aluminum. The floor consisted of 19 stainless steel rods 4 mm in diameter and 1.5 cm apart. Pellets were dispensed in a food trough located 2.1 cm above the floor and centered on a side wall. The house light was located 1.25 cm from the ceiling on the opposite

wall. A photocell unit inside the trough automatically recorded the number of head entries per second. Data was saved on a computer in the same room as the conditioning chambers.

The stimuli consisted of a tone CS at 80 dB and 1000 Hz and a white noise CS at 80 dB.

2.1.3. Procedure

2.1.3.1. Phase 1: Subjects were divided into two groups of eight. All subjects received a 12-second CS followed by a pellet. Half of the rats in each group received the tone CS, while the other half received the white noise CS. One group received an average ITI of 180s ranging from 105 to 255 seconds, and the other group received an average ITI of 360s ranging from 210 to 510 seconds. Both groups received 11 sessions of 15 trials (CS-US pairings).

2.1.3.2. Phase 2: For all rats, the CS duration was changed to 24s. The group that previously received a 180s ITI received a 360s ITI. The other group continued to receive a 360s ITI. Both groups received 20 sessions of 15 trials.

Table 1 shows the intervals received by each group throughout the experiment. In one group (15-15), the relative relationship, or ratio, between the CS and ITI intervals was maintained at 15 across phases, and in the other group (30-15), the relative relationship was changed. The group names indicate the ratios between the CS and ITI in Phase 1 and Phase 2 of the experiment.

2.2. Results

The number of head entries per second was used as a measure of responding. In order to determine how the pattern of responding changed across phases, we compared CS responding in the last five days of Phase 1 to CS responding in Phase 2. The analysis focused on the seconds of the CS that overlapped across phases, namely seconds 1 to 12 in the current experiment. Responding across the CS during baseline, Days 1 and 2 of Phase 2, and the last five days of Phase 2 are depicted for each group in Figure 1. As would be expected with an increase in CS duration, responding in seconds 1 to 12 decreased in Phase 2.

Adjustment to changes in the timing of reinforcement can be extremely rapid (Gallistel et al. 2001). To determine if either group significantly changed its responding in the first day of exposure to the new intervals, we compared responding in Day 1 of Phase 2 to baseline responding. First, in order to determine baseline responding for each rat, average elevation scores for the last 5 days of Phase 1 were computed for each subject. The average rate of responding in the 12 seconds preceding the CS was subtracted from the average rate of responding in each second of the 12s CS. These 12 elevation scores were then averaged into one summary baseline score for each rat. Second, an average elevation score for seconds 1 to 12 of the CS during Day 1 of Phase 2 was calculated in a similar manner for each rat, and this score was compared with the summary elevation score for the baseline period. These analyses indicated that in Day 1, Group 15-15 did not decrease its responding significantly from baseline, $t(7) = -1.10$, $P = .31$, but Group 30-15 did, $t(7) = -3.73$, $P = .007$. The same analysis was conducted to compare average elevation scores for the first five trials of Phase 2 with baseline elevation scores, and responding had not changed significantly in either group in the first five trials.

Furthermore, we also compared the groups in the amount of change in responding in Day 1. First, for each trial of Day 1 for each rat, elevation scores for seconds 1 to 12 of the CS were averaged into one score for each trial. Second, in order to track trial-by-trial changes in responding, the previously described summary baseline score for each rat was subtracted from each rat's elevation score for each trial. This difference score represented the amount of change

from baseline in each trial of Day 1. Fifteen scores per rat (one for each trial) were entered into a Group X Trial ANOVA with Trial as a repeated measure. There was a significant effect of Trial, $F(14, 196) = 3.25, p < .001$, indicating that the rats changed their responding over the course of Day 1. As illustrated in Figure 2, Group 30-15 appeared to display greater change in Day 1 than Group 15-15, but that was not a significant difference $F(1, 14) = 2.76, p = .12$. There was also no significant interaction between Trial and Group, $F(14, 196) = .43, p = .97$.

2.3. Discussion

If the animals transferred a relative temporal representation from Phase 1 to Phase 2, then we would expect Group 15-15, which received the same temporal ratio across phases, to display greater behavioral adjustment than Group 30-15 when first experiencing the new intervals in Phase 2. However, when the groups were compared in Day 1 of Phase 2, they did not differ in the amount of change from baseline. Therefore, this experiment did not provide evidence that animals transfer a relative representation of intervals to new durations. In fact, within-group analyses suggested that Group 30-15, which received a new temporal ratio in Phase 2, changed significantly from baseline in Day 1, while Group 15-15 did not.

Because all animals were transferred to a longer CS in Phase 2, their initial experience with the new durations included extinction of the old reinforced time. This extinction effect may have caused the animals to form new temporal memories in Phase 2, rather than rescale the acquired temporal representation (Bouton 2004). If the transfer from Phase 1 to Phase 2 were not to involve extinction, it is possible that a relative temporal representation might be more easily transferred to new intervals in Phase 2. We investigated this possibility in Experiment 2 by decreasing, rather than increasing, the CS duration across phases.

3. Experiment 2

In this experiment, rats received a shorter CS in Phase 2 than in Phase 1, thereby eliminating the possible extinction effect encountered in Experiment 1. One group received a maintained temporal ratio across phases, and the other received a changed ratio.

3.1. Materials and methods

3.1.1. Subjects—Subjects were 16 male Sprague-Dawley rats from the Charles River laboratories with no prior experimental history. They received the same housing conditions as the rats in Experiment 1.

3.1.2. Apparatus—The conditioning chambers were the same as those used in Experiment 1. The stimulus was a 1000 Hz tone at 80 dB.

3.1.3. Procedure—Subjects were divided into two groups of eight. The relative relationship, or ratio, between the CS and ITI intervals was maintained across phases in Group 15-15 and was changed in Group 7.5-15. Table 1 shows the intervals received by each group in each phase of the experiment.

3.1.3.1. Phase 1: Both groups received trials in which a 24s tone CS was followed by a pellet. Group 15-15 received an average ITI of 360s ranging from 240 to 480 seconds. Group 7.5-15 experienced an average ITI of 180s ranging from 105 to 255 seconds. All animals received 20 sessions of 15 trials.

3.1.3.2. Phase 2: All subjects were switched from a 24s CS to a 12s CS. Both groups received an average ITI of 180s, and both received 20 sessions of 15 trials.

3.2. Results

Figure 3 depicts patterns of responding for Groups 15-15 and 7.5-15 during baseline, in Days 1 and 2 of Phase 2, and at the end of Phase 2. We again compared baseline responding with responding in Day 1 of Phase 2 in seconds 1 to 12 of the CS. As described in Experiment 1, we first determined if either group changed significantly from baseline in Day 1 of Phase 2. An average elevation score for the CS was calculated for each rat for Day 1, and this score was compared with an average elevation score for the baseline period. These analyses indicated that in Day 1, Group 15-15 increased its responding significantly from baseline, $t(7) = 2.86$, $P = .024$, moving towards its final pattern of responding. In contrast, Group 7.5-15 decreased significantly from baseline in Day 1, $t(7) = -3.83$, $P = .006$, moving away from its final pattern of responding. The same analysis was conducted to compare average elevation scores for the first five trials of Phase 2 with baseline elevation scores, and significant positive change was already evident in Group 15-15 within the first five trials of Phase 2, $t(7) = 5.59$, $P = .001$, whereas responding had not yet changed significantly in Group 7.5-15, $t(7) = -1.25$, $P = .90$.

As in Experiment 1, to compare group performances in Day 1, difference scores were calculated for each rat between an average elevation score for the last five days of Phase 1 and an average elevation score for each trial of Day 1 of Phase 2. There was a significant effect for Group, $F(1, 14) = 18.91$, $p = .001$. As displayed in Figure 4, Group 15-15 displayed greater change from baseline in the expected direction in the first day of Phase 2 than Group 7.5-15. However, no significant effect was found for Trial, $F(14, 196) = 1.45$, $p = .13$, or for an interaction between Trial and Group, $F(14, 196) = 1.50$, $p = .12$.

3.3. Discussion

In Experiment 1, maintaining the ratio between the CS and ITI durations across phases did not facilitate behavior change in Phase 2. There may have been an extinction effect which prevented animals from transferring the acquired temporal relationship to the new intervals. In contrast, when this effect was eliminated in the current experiment, only the group receiving a maintained ratio in Phase 2 increased its responding in Day 1 of Phase 2, moving towards its final pattern of responding. In fact, this shift in responding began rapidly, within the first five trials of Day 1 of Phase 2. These results provide some evidence that rats may form representations of relative time in Pavlovian conditioning.

4. Experiment 3

In this experiment, we determined if the effects of the previous experiments would be stronger if subjects were challenged with a larger change in absolute durations. Rather than doubling or halving the CS across phases, the CS changed by a factor of three. Two groups received an increase in the CS from 8s to 24s, and two groups received a decrease from 24s to 8s.

4.1. Materials and methods

4.1.1. Subjects—Subjects were 32 male Sprague-Dawley rats from the Charles River laboratories with no prior experimental history. They received the same housing conditions as the rats in Experiments 1 and 2.

4.1.2. Apparatus—The conditioning chambers were the same as those used in the previous experiments. The stimulus consisted of a 1000 Hz tone at 80 db.

4.1.3. Procedure—Subjects were divided into four groups of eight. In Groups CS Up, the CS duration increased across phases, and in Groups CS Down, the CS duration decreased across phases. In each pair of groups, there was one group in which the relative relationship, or ratio, between the CS and ITI intervals was maintained across phases and one in which the relative

relationship was changed. Table 1 summarizes the intervals received by the groups in each phase of the experiment.

4.1.3.1. CS Up Groups: In Phase 1, the two CS Up groups received an 8s tone CS followed by a pellet. CS Up 15-15 received an average ITI of 120s, ranging from 70s to 170s, and CS Up 45-15 received an average ITI of 360s, ranging from 210s to 510s. Both groups received 20 sessions of 15 trials.

In Phase 2, the CS Up groups switched from an 8s CS to a 24s CS. They received an average ITI of 360s, ranging from 210s to 510s. The groups received 10 sessions of 15 trials.

4.1.3.2. CS Down Groups: In Phase 1, the two CS Down groups received a 24s tone CS followed by pellet delivery. CS Down 15-15 received an average ITI of 360s, ranging from 210s to 510s, and CS Down 5-15 received an average ITI of 120s, ranging from 70s to 170s. Both groups received 20 sessions of 15 trials.

In Phase 2, the CS Down groups switched from a 24s CS to an 8s CS. They received an average ITI of 120s, ranging from 70s to 170s. The two groups received 10 sessions of 15 trials.

4.2. Results

As in the previous experiments, we examined responding in the seconds of the CS that overlapped across both phases of the experiment. Thus, seconds 1 to 8 were the focus of this analysis. For the CS Up groups, patterns of CS responding at the end of Phase 1, the beginning of Phase 2, and the end of Phase 2 are displayed in Figure 5. When average elevation scores for each rat in Day 1 of Phase 2 were compared to baseline scores, we found that neither Group 15-15, nor Group 45-15, changed its responding significantly from baseline on Day 1, $t(7) = .97$, $P = .37$ and $t(7) = -1.18$, $P = .28$. Similarly, neither group changed its responding significantly from baseline in the first five trials of Day 1, $t(7) = 1.72$, $P = .13$ and $t(7) = -1.15$, $P = .29$. In addition, when the groups were compared on changes from baseline in each trial of Day 1, the groups did not differ significantly from each other, $F(1, 14) = 2.31$, $p = .15$ (Figure 6). Though there was a significant effect for Trial, $F(14, 196) = 3.43$, $p < .001$, there was no significant interaction between Trial and Group, $F(14, 196) = 1.25$, $p = .24$.

For the CS Down groups, elevation scores across the CS during baseline, the beginning of Phase 2, and the end of Phase 2 are displayed in Figure 7. When the analyses were repeated, we found that Group 15-15 increased its responding significantly from baseline in Day 1, $t(7) = 3.68$, $P = .008$, moving towards its final pattern of responding. In contrast, Group 5-15 displayed a nonsignificant decrease in responding in Day 1, $t(7) = -2.25$, $P = .059$. In addition, when each rat's average elevation score for the first five trials of Phase 2 was compared with its average baseline score, significant positive change was evident in Group 15-15 within the first five trials, $t(7) = 3.24$, $P = .014$, whereas responding had not yet changed significantly in Group 5-15, $t(7) = -.55$, $P = .60$.

When the CS Down groups were compared to each other in their change from baseline across the fifteen trials of Day 1 of Phase 2, it was found that Group 15-15 changed more from baseline towards the final pattern of responding in Day 1 than Group 5-15, $F(1, 14) = 18.40$, $p = .001$. However, there were no significant effects on Day 1 for Trial, $F(14, 196) = .49$, $p = .94$, or for the interaction between Trial and Group, $F(14, 196) = 1.15$, $p = .32$. The difference scores for the CS Down groups are displayed in Figure 8.

4.3. Discussion

In this experiment, maintaining the temporal ratio between the CS and ITI facilitated change when the CS decreased across phases, but not when it increased. This result is consistent with the previous two experiments. When the new CS is longer than the previous CS, there appears to be an extinction effect, leading to the abandonment of the previously acquired temporal representation. When the new CS is shorter, rats appear to transfer the acquired temporal ratio to the new intervals, thereby facilitating rapid adjustment in responding, even within five trials.

5. General Discussion

Taken as a whole, these experiments suggest that under some circumstances, rats may encode relative temporal representations in Pavlovian conditioning paradigms and transfer these representations to new intervals. Temporal representations may be transformed in scale to fit new absolute durations in the manner that spatial representations can be transformed in scale to fit new absolute distances. In addition, our results bear resemblance to Brannon and Terrace's findings (1998 (2000)) that rhesus monkeys can transfer ordinal information to new numerosities. That is, rhesus monkeys previously trained to order a set of numerosities transferred the judgment of relative position on a list to novel numerosities. In our experiments, animals transferred temporal ratios to novel intervals. When the novel intervals were shorter than the originally encoded intervals, animals receiving a maintained temporal ratio in the novel intervals displayed greater behavior change towards their final pattern of responding in the first day than animals receiving an altered ratio.

In contrast, when the new intervals were longer than the acquired intervals, maintaining the temporal ratio did not facilitate transfer to new intervals. In this case, the animals appeared to form new temporal maps, rather than transform the old ones. It seems likely that the extinction of the previously rewarded interval caused the learning of a new representation. When the original time of reinforcement passed without reward in the new CS, the animals may have regarded the new intervals as entirely novel, rather than as a transformation of the old intervals.

There may be alternative explanations for our results. For example, it is possible that behavioral momentum (Nevin 1979) contributes to the ease with which patterns of responding change. In this view, higher overall rates of reinforcement during baseline might lead to greater resistance to change. While the theory is usually used to explain resistance to change in overall rates of responding, it might also help to explain resistance to change in temporal patterns of responding.

As applied to our experiments, behavioral momentum theory might suggest that animals receiving a higher rate of reinforcement in Phase 1 in the form of shorter ITIs would display greater resistance to change in Phase 2. These animals would display comparatively less behavior change in Day 1 in response to the new intervals than animals that had received longer ITIs in Phase 1. In fact, this result was obtained. In our experiments, the animals receiving shorter ITIs in Phase 1 tended to display less change at the beginning of Phase 2 towards the final pattern of responding. In a similar vein, perhaps US density in Phase 1 defines a temporal context, and changing the context in Phase 2 might result in less interference from prior learning and an easier transition to a new pattern. However, it is admittedly speculative at this point as to whether theories about behavioral momentum or temporal context can be properly applied to changes in temporal patterns of responding – a question which can only be answered with further research.

In conclusion, our experiments provide conditional evidence for the encoding and transfer of relative temporal relationships in Pavlovian conditioning. Relative representations, whether temporal or spatial, allow animals to quickly adjust to new situations, instead of facing every

encounter as an entirely new one. In the natural world, distances and times are often redundant. For example, it would be adaptive to know that if a predator is only half the distance away as it was in a previous encounter, then one may have only half the time to execute an escape response. The relative representation of both space and time allows this sort of flexibility.

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Figure 1a

Figure 1b

Figure 1.

Experiment 1: Elevation scores across the CS in the last five days of Phase 1, Days 1 and 2 of Phase 2, and the last five days of Phase 2 for: (a) Group 15-15 and (b) Group 30-15. Rats received a 12s CS in Phase 1 and a 24s CS in Phase 2. In the first 12 seconds, responding decreased in Phase 2 to reflect the new, longer CS. (Error bars have been removed from this figure and similar figures for visual clarity.)

Figure 2.

Experiment 1: Difference between responding in each trial of Phase 2 Day 1 and in Phase 1 baseline. Group 30-15 changed more from baseline in the first day of receiving the new intervals than Group 15-15, but not significantly so.

Figure 3a

Figure 3b

Figure 3.

Experiment 2: Elevation scores across the CS in the last five days of Phase 1, Days 1 and 2 of Phase 2, and the last five days of Phase 2 for: (a) Group 15-15 and (b) Group 7.5-15. Rats received a 24s CS in Phase 1 and a 12s CS in Phase 2. In seconds 1 to 12, responding increased in Phase 2 to reflect the new, shorter CS.

Figure 4.

Experiment 2: Difference between responding in each trial of Phase 2 Day 1 and in Phase 1 baseline. Only Group 15-15 increased from baseline in Day 1, moving towards its final pattern of responding. The difference between the groups was significant ($p = .001$).

Figure 5a

Figure 5b

Figure 5.

Experiment 3, CS Up: Elevation scores across the CS in the last five days of Phase 1, Days 1 and 2 of Phase 2, and the last five days of Phase 2 for: (a) Group 15-15 and (b) Group 45-15. Rats received an 8s CS in Phase 1 and a 24s CS in Phase 2.

Figure 6.

Experiment 3, CS Up: Difference between responding in each trial of Phase 2 Day 1 and in Phase 1 baseline. Group 45-15 changed more from baseline in Day 1 than Group 15-15, but not significantly so.

Figure 7a

Figure 7b

Figure 7.

Experiment 3, CS Down: Elevation scores across the CS in the last five days of Phase 1, Days 1 and 2 of Phase 2, and the last five days of Phase 2 for: (a) Group 15-15 and (b) Group 5-15. Rats received a 24s CS in Phase 1 and an 8s CS in Phase 2.

Figure 8.

Experiment 3, CS Down: Difference between responding in each trial of Phase 2 Day 1 and in Phase 1 baseline. Only Group 15-15 increased from baseline in Day 1, moving towards its final pattern of responding. The difference between the groups was significant ($p = .001$).

Table 1

Durations of intervals received by each group in Phases 1 and 2

Experiment Number	Group Name	Phase 1 CS (s)	Phase 1 ITI (s)	Phase 2 CS (s)	Phase 2 ITI (s)
1	15-15	12	180	24	360
1	30-15	12	360	24	360
2	15-15	24	360	12	180
2	7.5-15	24	180	12	180
3	CS Up 15-15	8	120	24	360
3	CS Up 45-15	8	360	24	360
3	CS Down 15-15	24	360	8	120
3	CS Down 5-15	24	120	8	120