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4

Overshadowing and Stimulus Duration

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In 3 experiments, the authors investigated the effect of stimulus duration on overshadowing. Experiments 1 and 2 examined responding to a target conditioned stimulus (CS1) when it was conditioned in compound with a coterminating overshadowing stimulus (CS2) that was longer, shorter, or of the same duration (the long, short, and matched groups, respectively). Equal overshadowing of conditioning to CS1 was obtained in all 3 conditions relative to a control group conditioned to the light alone. There were, however, differences in responding to CS2 as a function of its absolute duration. Experiment 3 examined the contribution of the food–food interval/CS onset–food interval ratio to these findings. In Experiments 1 and 2, the ratio differed for the overshadowing CS but not for the target CS. In Experiment 3, this arrangement was reversed, but the pattern of results remained the same. The implications of these findings for trial-based and real-time models of conditioning are discussed.

Keywords: classical conditioning, overshadowing, stimulus duration, timing, rats

Cue competition refers to a basic set of learning phenomena that has attracted considerable empirical and theoretical interest (e.g., overshadowing; Pavlov, 1927; blocking; Kamin, 1969; relative validity; Wagner, Logan, Haberlandt, & Price, 1968). Of these related paradigms, in terms of basic experimental design, overshadowing is perhaps the most conceptually straightforward. In a typical overshadowing experiment, a target stimulus, the first conditioned stimulus (CS1), is conditioned in compound with a second stimulus, CS2, which is usually of the same duration as CS1, with both stimuli terminating with the delivery of an unconditioned stimulus (US). The typical finding is that responding to CS2 interferes with the acquisition of conditioned responding to CS1, in that responding to this stimulus is attenuated in comparison to conditioning of CS1 in isolation.

A critical factor in overshadowing is the relative salience of the CSs that compete for associative strength (e.g., Mackintosh, 1976); that is, the more salient CS2 is, the more likely it is to overshadow its companion, CS1. One interpretation of this observation is that overshadowing represents a mechanism whereby organisms learn about the most efficient or useful predictor of the impending US;

a more salient and thus more noticeable CS could be regarded as a more effective signal than a less salient CS. From this perspective, one might expect that other features of the stimuli could influence the magnitude of the overshadowing effect. One plausible candidate is CS duration: If two CSs differ in duration and coterminate with US delivery, then their different durations might render one a more efficient predictor of the outcome than the other. For example, one could argue that onset of the first CS renders the second redundant as a predictor of the US, so the animal might reasonably learn about a longer CS at the expense of learning about a shorter CS (e.g., Egger & Miller, 1962; Seger & Scheuer, 1977). In support of this position, Egger and Miller conditioned a 2-s stimulus in compound with a 1.5-s stimulus, such that both coterminated with US delivery, and assessed responding to the two stimuli. They found higher levels of responding to the longer stimulus. However, in a control condition in which the long CS's ability to predict food was degraded (by the addition of trials in which it was presented alone without reinforcement), the advantage of the longer stimulus was attenuated, and subjects responded significantly more to the shorter stimulus than did subjects in the experimental group. Although the experiment did not include an overshadowing control group, the results are consistent with the suggestion that the longer CS overshadowed the shorter one. The authors interpreted their findings in terms of an informational hypothesis, postulating that the nonredundant information conveyed by a stimulus is critical for engaging the learning process (c.f. Rescorla & Wagner, 1972). According to this hypothesis, in the experimental condition the shorter CS did not convey any additional information about US delivery, which resulted in its failure to acquire associative strength (Cantor, 1981).

A more recent mathematical model of conditioning, the temporal difference (TD) model (Sutton & Barto, 1990), provides a mechanism for producing these effects. According to the TD

model, each stimulus consists of a series of units that are independently conditioned. The conditioning mechanism is a modification of the Rescorla–Wagner model (Rescorla & Wagner, 1972), but with competition occurring among component units of the CSs rather than at trial level. When CSs are matched in duration, the numbers of competing units within the CSs are also matched, but when one stimulus is longer, that CS acquires more associative strength because it has units that are free from direct competition with units of the shorter CS. Consequently, a longer CS should overshadow a shorter one.

However, other findings imply the opposite—that the shorter stimulus is the more useful predictor and overshadows the longer one. For example, Kehoe (1983) found that overshadowing of rabbit nictitating membrane conditioning was attenuated when the target CS was shorter than the overshadowing stimulus, compared to when the CSs were matched in duration (see also Fairhurst, Gallistel, & Gibbon, 2003; Hancock, 1982). These results are consistent with the *time-of-arrival hypothesis* (Goddard & Jenkins, 1988), which states that, all other things being equal, there will be preferential learning about the shorter of two stimuli, since it is easier to predict the time of US delivery with a shorter CS. However, this finding highlights a critical confound in some of these experiments—that shorter CSs tend to elicit greater levels of conditioned responding than longer ones (e.g., Holland, 2000; Kirkpatrick & Church, 2003; Lattal, 1999). This consideration casts doubt on those studies that have suggested that shorter stimuli are better at overshadowing. Moreover, the different studies we have considered employed different absolute stimulus durations—which could, in itself, influence the likelihood of observing an overshadowing effect.

It is unclear from the preceding review whether the shorter or the longer element of a stimulus compound is better at overshadowing. One reason for this uncertainty lies in the fact that virtually no studies have addressed the question directly while also controlling for the effects of absolute stimulus duration on response rate. The rationale for the present studies is therefore twofold. The first aim is to undertake a more systematic investigation of the effects of stimulus duration on overshadowing in a procedure that controls for the absolute duration of the target stimulus and does not rely on cross-experiment comparisons. In each of the studies below, the target stimulus (CS1) was always a fixed duration, and the duration of the overshadowing stimulus (CS2) was manipulated so that it was either longer than, shorter than, or the same duration as the target CS. This permitted the assessment of whether CS2 duration would affect the degree of overshadowing of CS1 without any confounding effects of CS1 duration on responding. The timing models outlined above both make explicit predictions about the outcome of these experiments: According to the TD model, overshadowing should be maximal when CS2 is longer than CS1, whereas according to the time-of-arrival hypothesis, overshadowing should be maximal when CS2 is shorter than CS1.

A second aim of these experiments is to examine timing during overshadowing. There is a substantial literature demonstrating that in the course of classical conditioning, animals learn not only that an outcome will occur but when that outcome will occur—timing. This learning is evident in that response rates increase over the course of the stimulus to a maximum near the time of food delivery (e.g., Kirkpatrick & Church, 2000), and if the stimulus is extended in a nonreinforced trial (the peak procedure), responding falls

again, with a peak at the time when food would normally occur (Kirkpatrick & Church, 2000).

While timing during individual stimuli is well understood, there has been little investigation of the effects of cue competition on this process (but see Jennings & Kirkpatrick, 2006). There has been much recent theoretical interest in merging conditioning and timing within the framework of a single process model (e.g., Gallistel & Gibbon, 2000; Goddard & Jenkins, 1988; Kirkpatrick, 2002; Savastano & Miller, 1998; Sutton & Barto, 1990); however, little is known about the effects of basic conditioning manipulations on timing. If these hybrid theoretical approaches are to be developed further, it would be useful to know whether cue competition affects timing of the CS duration as well as attenuating the magnitude of the conditioned response. At face value, the standard associative model predicts that if timing is a product of conditioning and conditioning is attenuated by cue competition, then the ability to time should also be compromised. Accordingly, the present experiments examine whether the impairment in acquisition of associative strength seen in an overshadowing paradigm is accompanied by impairments in timing of that stimulus and also whether any such effects are influenced by the duration of the overshadowing stimulus.

Experiment 1

Four groups of rats were conditioned to a 20-s light stimulus that signaled food delivery. In three of the groups, the light was accompanied by white noise, and these two stimuli coterminated with food delivery; in the control group, the light was conditioned in isolation. The duration of the noise differed in the three experimental groups: In the short group (Group S) it was half the duration of the light (10 s), whereas in the long group (Group L) it was double the light's duration (40 s); in the matched group (Group M) their durations were the same (20 s). The question of interest was the degree to which these different duration stimuli would overshadow conditioning to the light. The TD model predicts the most overshadowing in Group L and the least in Group S, whereas the time-of-arrival hypothesis makes the opposite prediction. We also examined the time course of responding during the various stimuli to investigate whether timing was subject to overshadowing and whether timing accuracy was affected by the duration of the overshadowing stimulus.

Method

Subjects

The subjects were 32 male Lister hooded rats (*Rattus norvegicus*; Harlan Olac Ltd., Oxfordshire, England), which were housed in pairs in a colony room on a 12-hr light:dark cycle (lights on at 8 am). The rats had a mean free-feeding weight of 365 g (range = 355–405 g) and were maintained at 80% of this level by being fed a restricted amount of food following each experimental session. Water was available ad libitum in both the home cages and the experimental chambers. Rats were handled and weighed daily in the colony room. All rats had previous experience of an unrelated (flavor conditioning) procedure performed in the home cage but were naive to all aspects of the current experiment.

Apparatus

Each of the 12 chambers ($25 \times 30 \times 30$ cm) was located inside a ventilated, noise-attenuating box ($74 \times 38 \times 60$ cm). The chambers were housed in two separate rooms, with 6 chambers located in each room. Each chamber was equipped with a speaker for delivering auditory stimuli, which was located at the top of the right wall of the chamber, on the opposite side to the food cup, and delivered a 70-dB white noise that was used as the overshadowing stimulus (CS2). There was no background illumination. A jewel light (Model ENV-227M, Med Associates, St. Albans, VT), which was located above the food cup, provided diffuse illumination of approximately 200 lux. This cue was used as the target stimulus (CS1). A magazine pellet dispenser (Model ENV-203, Med Associates) delivered 45-mg Noyes (Lancaster, NH; Improved Formula A) pellets into a food cup. Each head entry into the food cup was recorded by interruption of an LED photocell. A water bottle was mounted outside the chamber directly opposite to the food cup, and water was accessed via a tube that protruded through a hole in the 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

Training (Sessions 1–6). Rats were randomly assigned to one of four groups (ns = 8), all of which received presentations of a 20-s light stimulus immediately followed by the delivery of a single food pellet. All subjects received 26 conditioning trials per session; for the control group (Group C) these were only presentations of the light, whereas in the remaining three groups the light was accompanied by the white noise and both stimuli coterminated with food delivery. For Group S the noise lasted 10 s, for Group M it lasted 20 s, and for Group L it lasted 40 s. The intertrial interval (ITI; measured from food delivery to the first stimulus onset on the following trial) was a fixed 60 s plus a random 60 s, which yielded sessions that were approximately 1 hr in duration. There were no noise, light, or food deliveries during the ITI.

Testing (Sessions 7–16). Following the six training sessions, Groups S, M, and L received sessions containing three different trial types—20 reinforced compound trials exactly like those delivered during the previous stage, 3 presentations of the noise alone, and 3 presentations of the light alone. In each group, the noise and light probe trials were the same duration as presentations of those same stimuli during compound trials (i.e., the light was 20 s in all groups, and the noise was 10 s, 20 s, and 40 s in Groups S, M, and L, respectively), and all terminated with the delivery of a food pellet. Group C continued to receive 26 trials with the light, 3 of which were arbitrarily selected as probe trials for purposes of comparison with the light-only probe trials of the three compound groups.

Data Analysis

The time of occurrence of each stimulus onset, stimulus termination, food delivery, and head entry response was recorded with a time stamp, with a resolution of 2 ms. The raw data were analyzed in MatLab (MathWorks, 2005), and statistical analysis of the various summary measures was conducted in SPSS (Version 12). A significance level of .05 was adopted in all the analyses outlined below; all post hoc analyses were conducted with Tukey's honestly significant difference test.

Conditioning in the training and test phases was recorded in two-session blocks. We analyzed conditioning in each block during the test phase by determining the mean response rate during the CS for a particular trial type (compound, light probe, noise probe). Pre-CS response rates were also recorded for each probe trial; in Experiments 1 and 2 the duration of the pre-CS period was matched to the target CS duration (20 s in Experiment 1 and 30 s in Experiment 2). In Experiment 3, a 10-s pre-CS period was used throughout; this was because the shortest ITI (in Group S) was 10 s.

Timing was assessed during compound trials and during the light and noise probe trials in the test phase. We conducted analyses of temporal control of behavior by determining the number of head entry responses that occurred in successive 1-s time bins during the CS, pooled across all sessions of the relevant phase. The response rate functions were then normalized so that each rat would contribute equally to the shape of the functions, regardless of its overall response rate: The response rate in each time bin was divided by the total number of responses and multiplied by 100 to give the percentage of total responses in each time bin for each subject.

We conducted analysis of the slope of the response rate functions, as an index of timing accuracy, by fitting a linear function to the normalized response rate functions. The slope was then determined from the best fitting linear curve for each response rate function. Linear fits were used because these provide a good characterization of the response rate functions. For between-groups comparisons of the slopes, the fits were constrained to the first 10 s to equate for the effect of opportunity to respond on the normalized response rates.

Results

Probe Trials

Target stimulus (light) conditioning. From a visual inspection of Figure 1 (top left panel), Group C responded at a higher rate **F1** than the other three groups, indicating that overshadowing had occurred. There was little difference in responding between Groups M and S, but responding in Group L appeared to be slightly lower than in the other two overshadowing groups. An analysis of variance (ANOVA) comparing the four groups over the five 2-session blocks of this phase showed that there was a significant effect of block, $F(4, 112) = 3.1$, $p < .05$, but no Block $\times$ Group interaction ($F < 1$). There was a significant main effect of group, $F(3, 28) = 7.3$, $p < .001$; Tukey's post hoc analyses indicated that Group C had a significantly higher rate of responding than the other three groups, which did not differ. These results indicate that overshadowing was obtained but that it did not differ as a function of the duration of the overshadowing stimulus.

Target stimulus (light) timing. As in training, all four groups displayed an increase in the rate of responding over the course of light presentations, as shown in Figure 1 (top right panel), indicating that the animals had learned to use onset of the light CS to anticipate food delivery. A one-sample t test revealed that the
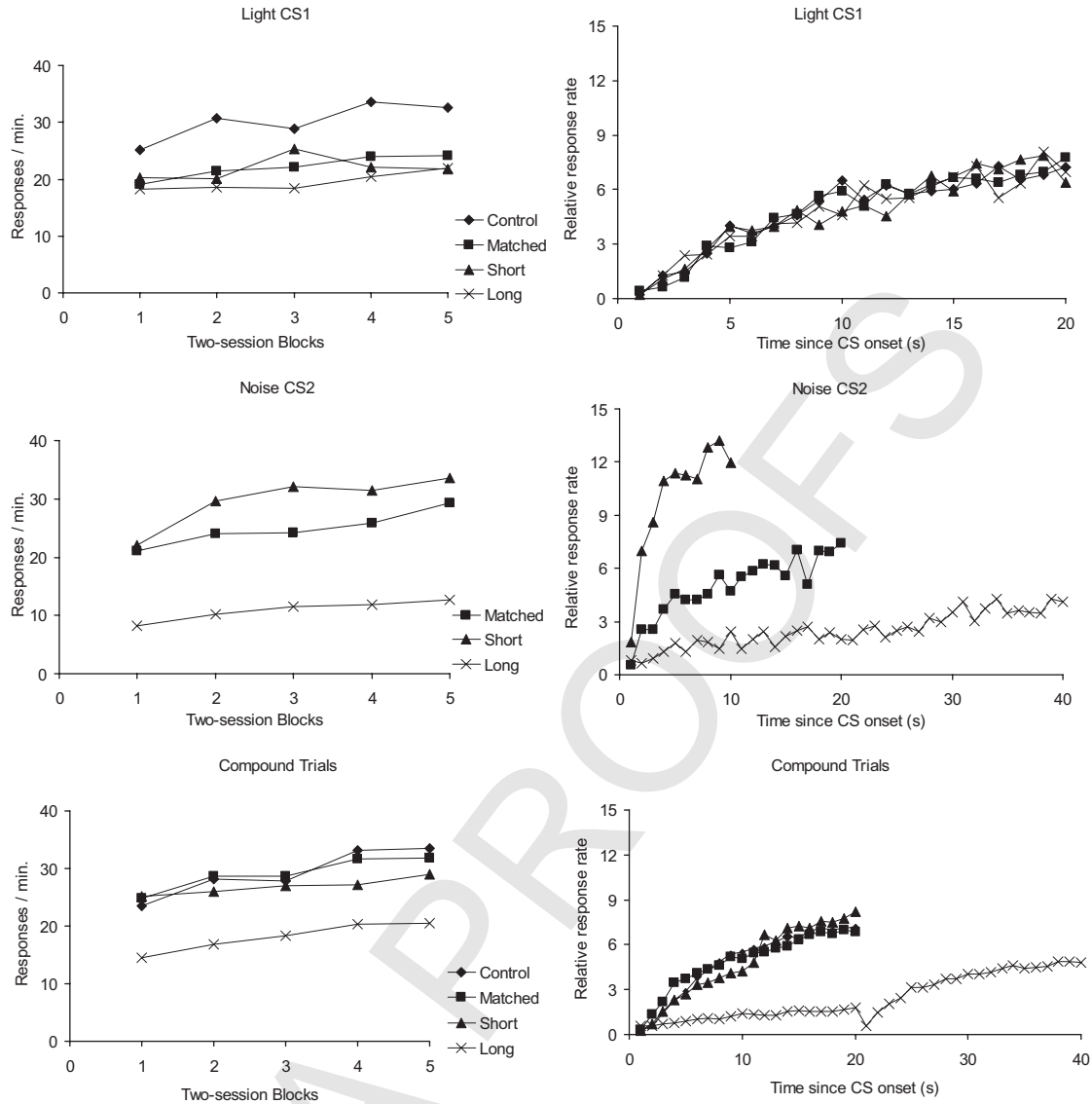
Figure 1. Experiment 1. Left column: The mean rate of responding during probe trials (responses per minute) to the target stimulus (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel) over five 2-session blocks. Right column: The relative rate of responding as a percentage of the total responses over stimulus duration during reinforced probe trials of the target (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel). CS = conditioned stimulus.

slopes of responding in each group differed significantly against a slope of zero: Group C, $t(7) = 10.4$; Group M, $t(7) = 7.8$; Group S, $t(7) = 6.5$; Group L, $t(7) = 9.6$. An ANOVA comparing these slopes revealed no difference among them ($F < 1$), suggesting that each group timed the duration of the light with a similar degree of accuracy.

Overshadowing stimulus (noise) conditioning. A visual inspection of the rate of responding to the noise probes (Figure 1, middle left panel) indicated that Group L had the lowest rate of responding and Group S the highest. This is what would be expected on the grounds of their differing durations—it has been frequently observed that shorter stimuli elicit higher rates of responding than longer stimuli (e.g., Kirkpatrick & Church, 2000;

Holland, 2000; Lattal, 1999). An ANOVA comparing the response rates of the three groups over the 10 blocks revealed a significant main effect of block, $F(4, 84) = 5.4$, $p < .001$, but no Block × Group interaction ($F < 1$). As expected, there was a significant main effect of group, $F(2, 21) = 19.9$, $p < .001$, and post hoc tests indicated that Group L exhibited a lower response rate than Groups M and S, which did not differ.

Overshadowing stimulus (noise) timing. Inspection of Figure 1 (middle right panel) suggests that all groups learned to time the noise duration; the timing function was steepest in Group S and shallowest in Group L. These response rate functions are strikingly similar to timing functions recorded during simple delay conditioning procedures (e.g., Kirkpatrick & Church, 2000). One-

sample *t* tests indicated that the response slope in each group differed from zero: Group M, $t(7) = 8.7$; Group S, $t(7) = 6.8$; Group L, $t(7) = 7.0$. The corresponding means were 1.2, 0.9, and 1.1 for Groups M, S, and L, respectively. A comparison of the recalculated slopes indicated that there was no difference among the three groups ($F < 1$), demonstrating that timing accuracy was similar across the different stimulus durations.

Pre-CS Responding

The pre-CS period was defined as a 20-s period immediately preceding light probe trials. An analysis of pre-CS responding disclosed that the mean rates of responding were 2.4, 2.6, 1.6, and 4.9 for Groups C, M, S, and L, respectively, and these rates did not differ, $F(3, 28) = 2.5$.

Compound Trials

Responding during the compound trials in the test phase was relatively stable over the 10 test sessions; there was an increase in responding over blocks, $F(4, 112) = 16.2$, $p < .001$, but no Block × Group interaction ($F < 1$). There was a significant main effect of group, $F(3, 28) = 8.8$, $p < .001$, and post hoc tests indicated that Group L's responding was significantly lower than that in Groups C, M, and S, which did not differ (Figure 1, bottom left panel; data displayed refer to Sessions 7–16 in two-session blocks). This was probably an effect of stimulus duration, as longer stimuli tend to produce lower response rates. The timing data from the compound trials (bottom right panel of Figure 1) showed an increase in the rate of responding from CS onset to CS offset when food delivery was imminent, and these slopes differed from zero: Group C, $t(7) = 14.5$; Group M, $t(7) = 10.9$; Group S, $t(7) = 7.6$; Group L, $t(7) = 8.0$. Group L had the most shallow slope, but there was a sharp increase in responding following the onset of the target stimulus at 20 s. The other three groups displayed a rapid increase in responding that peaked at about the time of food delivery; this form of responding on the basis of CS duration is a typical characteristic of timing functions.

Discussion

The present experiment investigated whether overshadowing differed as a function of whether the overshadowing stimulus was longer than, shorter than, or matched in duration to the target. Two different models, the TD model and the time-of-arrival hypothesis, predict that overshadowing should be affected by this manipulation. However, although there was a significant overshadowing effect in all three groups, altering the duration of the overshadowing stimulus did not influence the magnitude of this effect.

Significant differences in conditioning to the overshadowing stimulus were, however, obtained in the experimental groups: Group L responded to the noise at a significantly lower rate than animals in Groups M and S. This observation does not follow from the TD model (Sutton & Barto, 1990), which predicts that when the noise stimulus is longer than the light it should acquire more of the available associative strength than when it is shorter; in fact, the opposite was observed (see also Jennings & Kirkpatrick, 2006, for a related finding in the blocking paradigm). The time-of-arrival hypothesis (Goddard & Jenkins, 1988) can, however, explain this

result, as it maintains that a shorter stimulus will command higher associative strength by virtue of the fact that it is a more accurate predictor of reinforcement. Although training two stimuli in compound produced a significant overshadowing effect, it did not interfere with acquisition of timing—there was no difference between the experimental and control groups in timing accuracy to the light. There was also an effect of stimulus duration on timing to the noise probes; overall, the slopes became steeper as stimulus duration decreased (e.g., Holland, 2000; Kirkpatrick & Church, 2000, 2003).

Two time-based conditioning models predicted that overshadowing stimulus duration would affect the degree of overshadowing obtained, but no evidence was found to support this assertion. The literature concerning the effects of cue competition on acquisition of timing is relatively sparse; our results are, however, consistent with reports from other cue competition paradigms that demonstrated intact timing despite observation of a blocking effect (Gaioni, 1982; Jennings & Kirkpatrick, 2006). Nevertheless, before we accept this conclusion, it seems prudent to pursue the issue further. Figure 1 suggests that, although the effect was not statistically significant, subjects in Group L appeared to respond to the light at a lower rate than those in Groups M or S. It is possible that had we introduced a greater difference in duration between the noise and light, we might have obtained a significant effect. Experiment 2 was designed to explore this possibility.

Experiment 2

Experiment 2 is a replication of Experiment 1, except that the duration of the target light stimulus was increased from 20 s to 30 s and the ratio of noise to light durations was 3:1 in Group L and 1:3 in Group S. Thus, the noise was 90 s in Group L and 10 s in Group S.

Method

Subjects

The subjects were 32 male Lister hooded rats (Harlan Orlac Ltd., Oxfordshire, England) with a mean free-feeding weight of 353 g (range = 335–420 g). They had previously served in an experiment on flavor aversion learning but were naive to all aspects of the current experiment. They were housed and maintained exactly as in Experiment 1.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

The procedures for the present experiment were identical to those employed in Experiment 1, with the exception of the duration of the stimuli used. As noted above, the target light stimulus duration was increased to 30 s, and the ratio between the overshadowing noise stimulus and the target was also altered. Thus, Group C received 30-s light trials and Group M a simultaneous compound of a 30-s light and 30-s white noise. The pre-CS period was 30 s for all groups.

Results

Probe Trials

Target stimulus (light) conditioning.   Responding to the light may be seen in Figure 2 (top left panel) pooled over two-session blocks; it is clear that rates were highest in Group C but that the other groups did not differ. An ANOVA with group and block as factors showed that there was no effect of block, nor was there any Group $\times$ Block interaction (both Fs $<$ 1). There was, however, a significant main effect of group, $F(3, 28) = 11.2$, $p < .001$; post hoc comparisons indicated that Group C responded at a significantly higher rate than Groups M, S, and L, which did not differ.

Target stimulus (light) timing.   Analysis of the response slopes during the light indicated that there was an increase in responding over CS duration that was similar in the four groups. One-sample t tests confirmed that the response slopes differed significantly from zero in all groups, smallest $t(7) = 10.4$ (Figure 2, top right panel); an ANOVA comparing the response slopes of the four groups indicated that they did not differ, $F(3, 28) = 1.1$.

Overshadowing stimulus (noise) conditioning.   Data from the noise probe trials are shown in Figure 2 (middle right panel), presented in two-session blocks. The highest response rates were evident in Group S and the lowest in Group L, with Group M intermediate. An ANOVA with group and block as factors revealed a significant effect of block, $F(4, 84) = 4.2$, $p < .01$; a significant effect of group, $F(4, 84) = 90.2$, $p < .001$; and a significant Group $\times$ Block interaction, $F(8, 84) = 2.6$, $p < .05$. Simple main effects revealed an effect of block in Groups M and
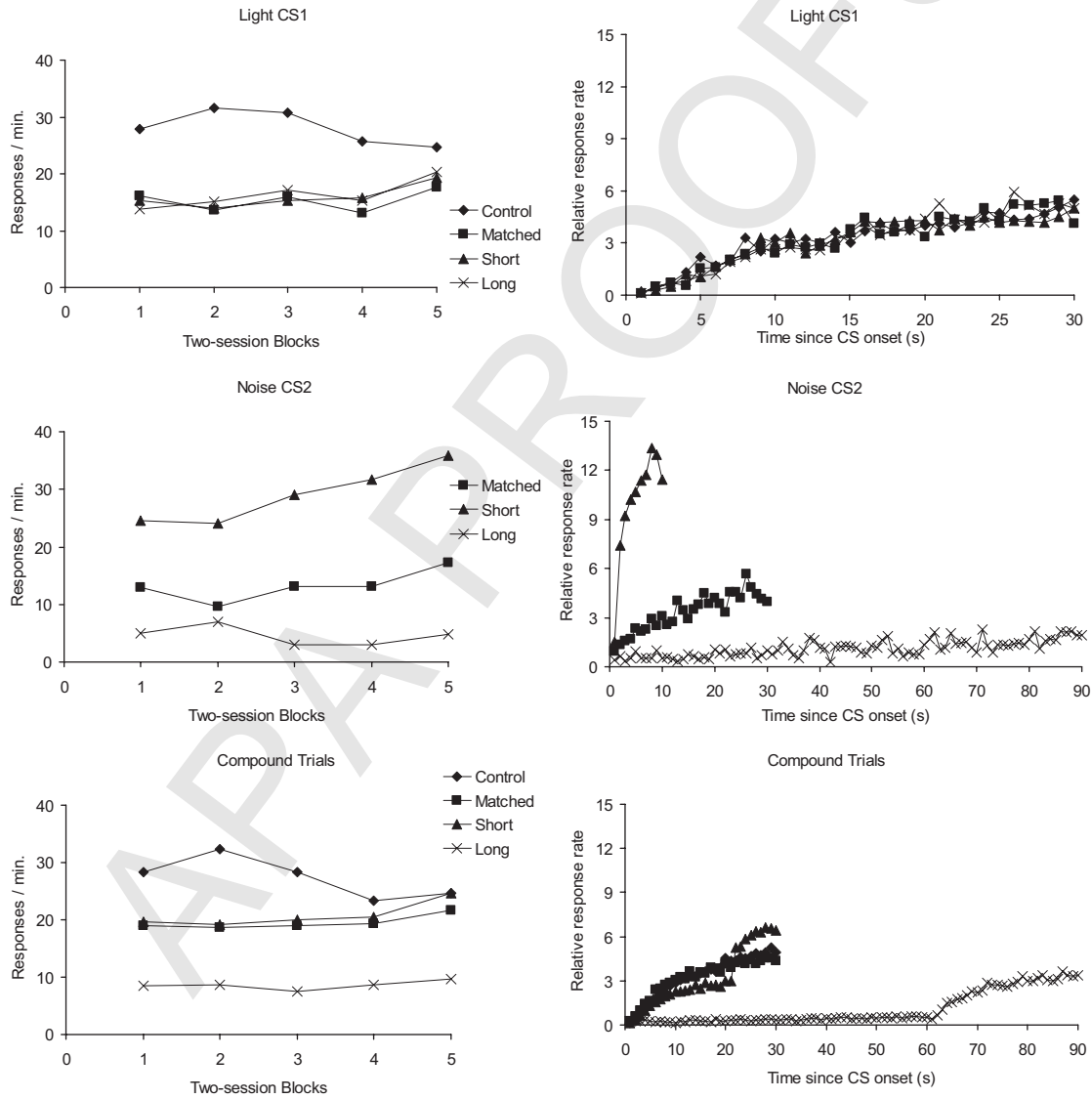

Figure 2.   Experiment 2. Left column: The mean rate of responding (responses per minute) to the target stimulus (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel) over five 2-session blocks. Right column: The relative rate of responding as a percentage of the total responses over stimulus duration during reinforced probe trials of the target (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel). CS = conditioned stimulus.

S, $F(4, 84) = 2.6$, $p < .05$, and $F(4, 84) = 5.7$, $p < .01$, respectively, but not in Group L ($F < 1$). There was also significant effect of group in all five blocks, smallest $F(2, 105) = 19.1$, $p < .01$. Post hoc tests performed on each two-session block revealed that all groups differed significantly from each other in all but Block 2, on which responding in Groups M and L did not differ.

Overshadowing stimulus (noise) timing. As with the light, the response slopes of the three experimental groups were all significantly greater than zero, smallest $t(7) = 5.5$ (Figure 2, middle left panel). As in Experiment 1, we recalculated the slopes to compare responding over the first 10 s of the noise probes, which yielded values of 1.1, 0.9, and 0.3 for Groups M, S, and L, respectively; these recalculated slopes did not differ, $F(2, 21) = 1.4$.

Pre-CS Responding

As with Experiment 1, pre-CS response rates were taken over an interval matched to the duration of the target stimulus (30 s in the present experiment). The mean rates of pre-CS responding were 2.1, 4.5, 3.5, and 1.7 for Groups C, M, S, and L, respectively, and these rates did not differ, $F(3, 28) = 2.3$.

Compound Trials

Rates of responding were broadly similar to those observed in Experiment 1; subjects in Groups M and S showed similar levels of responding, while those in Group C displayed higher response rates and those in Group L responded somewhat less. ANOVA indicated that there was no effect of block ($F < 1$), nor was there a Block × Group interaction, $F(12, 112) = 1.4$. There was a significant effect of group, $F(3, 28) = 19.0$, $p < .001$; post hoc tests showed that Group L responded significantly less than Groups C, M, and S. Responding in Groups M and S did not differ, while Group C responded significantly more than the other three groups (see bottom left panel of Figure 2). As in Experiment 1, responding increased over the duration of the stimulus, reaching a peak at about the time of US delivery, and the slopes differed from zero, smallest $t(7) = 8.8$ (see bottom right panel of Figure 2). The longer stimulus durations employed in the present experiment highlight the transition in responding from a single stimulus to a compound of the two stimuli. At the onset of the second stimulus, there was a rapid increase in responding in Groups S and L.

Discussion

The results of the present experiment concur with those reported in Experiment 1. There was significant overshadowing in all groups, and the size of this effect was not dependent on the duration of the overshadowing stimulus. However, there was evidence for a difference in conditioning to the overshadowing stimulus—the shorter the noise was, the higher was the level of conditioned responding that it was able to support. As in Experiment 1, this pattern of responding to the noise is consistent with the predictions of the time-of-arrival hypothesis.

It is also evident that all groups tracked the time to reinforcement during both the light and the noise probes. Although there is clear evidence that the animals exhibited overshadowing, this had no impact on their ability to time the light. These results confirm the findings of Experiment 1 that there was no evidence for overshadowing of timing.

One potential interpretation of these data is in terms of relative cycle time. Rate expectancy theory and its earlier variations (Gallistel & Gibbon, 2000, 2002; Gibbon & Balsam, 1981) explain conditioned responding in terms of a comparison of the overall rate of reinforcement in the background (food–food interval [C] or food–CS onset interval [I]) to that during the CS (CS onset–food interval [T]). Here, we concentrate on the original C/T ratio proposed by Gibbon and Balsam (1981); the same pattern would apply if we used the newer I/T formulation.

In both models, when the rate of reinforcement is perceived as being greater during the stimulus than during the background, responding occurs. The larger the C/T ratio is, the more information about food delivery is given by CS onset and the faster is the rate of acquisition. While rate expectancy theory was developed to predict the speed of acquisition of responding, it has been demonstrated that larger C/T ratios also yield higher response rates (e.g., Domjan, 1980; Gibbon, Baldock, Locurto, Gold, & Terrace, 1977; Kirkpatrick & Church, 2000; Lattal, 1999; Salafia, Terry, & Daston, 1975; although see Holland, 2000). This simple principle could explain many features of the present data, as in both experiments the ITI, which was measured from food delivery on one trial to the first CS onset on the next, was held constant. In Experiments 1 and 2, the C/T ratios were almost identical for the light but differed quite dramatically for the noise. In Experiment 1, the C/T ratios were 7, 7, and 10 for the light and 14, 7, and 2.3 for the noise in Groups S, M, and L, respectively. In Experiment 2, the C/T ratios for the light were 5, 5, and 7, whereas the corresponding values for the noise were 15, 5, and 2.3 for Groups S, M, and L, respectively.

This analysis can explain why response rates to the noise differed, while the response rates to the light were highly similar across groups. However, without introducing an additional principle of cue competition, the C/T ratio cannot explain why overshadowing occurred in Groups S, M, and L relative to Group C. In fact, rate expectancy theory does allow for some redistribution of strength between stimuli conditioned in compound on the basis of stimulus salience but not the basis of on their relative durations. Thus, if one were to argue that the results support an effect of C/T ratio superimposed on the overshadowing effect, then it should be possible to alter the relative response rates to the target and overshadowing stimuli by altering the C/T ratios appropriately. Experiment 3 was designed to evaluate this possibility.

Experiment 3

Experiment 3 was a replication of the three overshadowing groups of Experiment 2, with the exception that the ITIs were manipulated to equate the C/T ratios for the noise while introducing differences in the C/T ratios associated with the light—the converse arrangement to that in the previous two experiments. If our suggested analysis of Experiments 1 and 2 is correct, then this should produce similar response rates to the overshadowing stimulus, the noise, while group differences in responding to the light target stimulus should emerge. Accordingly, the ITI was altered to be an average of 20 s in Group S, 120 s in Group M, and 360 s in Group L. This would yield an identical C/T ratio of 4 in all groups

for the noise but differing C/T values for the light of 2, 4, and 12 for Groups S, M, and L, respectively.

Method

Subjects

The subjects were 24 experimentally naive male Lister hooded rats (Harlan Orlac Ltd., Oxfordshire, England) with a mean free-feeding weight of 300 g (range = 270–320 g). Because of their small size at the start of the experiment, the rats were maintained at 85% of their free-feeding weight throughout. All other aspects of housing and husbandry were the same as in Experiments 1 and 2.

Apparatus

The apparatus used was the same as in Experiments 1 and 2.

Procedure

There were three groups (*n*s = 8) in the present experiment, Groups M, S, and L, which corresponded to the three compound groups of Experiment 2. Their training was identical to that in Experiment 2 except for the ITIs employed, which were 10 s + variable 10 s in Group S, 60 s + variable 60 s in Group M, and 180 s + variable 180 s in Group L.

Training (Sessions 1–6). All aspects of training were identical to Experiments 1 and 2.

Testing (Sessions 7–16). The number and distribution of probe trials was the same as above.

Performance test (Sessions 17–18). To investigate the possibility that these differences in ITI might affect performance at test rather than learning, we also gave the animals two final test sessions in which the ITI durations in the three groups were matched to the value employed in Experiment 2 (60 s + variable 60 s); in all other respects, these sessions were identical to those of the previous phase.

Results

Probe Trials

Target stimulus (light) conditioning. A visual inspection of the data suggested that responding in Groups M and L remained relatively stable over the course of testing, while responding in Group S increased slightly (Figure 3, top left panel). However, an ANOVA with group and block as factors showed only a significant main effect of block, $F(4, 84) = 2.9$, $p < .05$; there was no effect of group, $F(2, 21) = 1.2$, or Group × Block interaction, $F(8, 84) = 1.5$.

Target stimulus (light) timing. There was an increase in responding over the duration of the light probes, and the slopes of responding differed significantly from zero in all three groups, smallest $t(7) = 7.2$, $p < .001$ (Figure 3, top right panel). There was no difference among the groups in response slope ($F < 1$).

Overshadowing stimulus (noise) conditioning. The highest level of responding to the noise probes was shown by Group S and the lowest level by Group L, with Group M intermediate (Figure 3, middle left panel); responding appeared to increase slightly over the course of testing. An ANOVA with group and block as factors

revealed a significant main effect of block, $F(4, 84) = 5.1$, $p < .001$, and also of group, $F(2, 21) = 11.2$, $p < .001$; there was no Group × Block interaction, $F(8, 84) = 2.0$. Post hoc tests indicated that Group L responded at a significantly lower level than Groups M and S, which did not differ.

Overshadowing stimulus (noise) timing. All groups displayed an increase in responding over the duration of the noise that peaked at about the time of food delivery (middle right panel of Figure 3). A comparison of the slopes of responding against zero confirmed that the increase in responding was significant in all three groups, smallest $t(7) = 6.3$, $p < .001$. There was no difference in the response slopes calculated over the first 10 s of the noise probes, $F(2, 21) = 1.4$ (mean values = 1.3, 1, and 0.6 for Groups M, S, and L, respectively), consistent with the results of Experiments 1 and 2.

Pre-CS Responding

Pre-CS rates were calculated over the 10-s period just prior to the onset of the target stimulus; this was equal to the minimum ITI duration in Group S. The mean rates of pre-CS responding were 3.1, 8.2, and 0.9 for Groups M, S, and L, respectively, and these rates differed significantly, $F(2, 21) = 24.6$; Tukey's post hoc tests revealed that responding in Group S (for which the ITI was 20 s, on average) was higher than that in the other two groups, which did not differ. This was probably because rats were consuming the previously delivered food pellet (e.g., see Figure 4 in Kirkpatrick & Church, 2000). However, this difference in pre-CS responding could have affected the response rates during the CS. To assess any such effects, we computed elevation scores by subtracting the pre-CS rates from the CS response rates. The elevation scores were 20.6, 10.9, and 16.1 for Groups M, S, and L, respectively. An ANOVA revealed a main effect of group, $F(1, 21) = 10.4$, $p < .001$. Post hoc tests (Tukey's honestly significant difference test) showed that Group M differed significantly from Group S; Group L did not differ from either Group M or Group S. However, the elevation scores suffered from the issue that it is not entirely appropriate to compare elevation from different baselines. To address this issue, we conducted a final performance test.

Performance Test

To assess whether the test results were the product of a performance effect stemming from the group differences in ITI duration, rather than an effect on learning, we compared the mean response rates to the light and the noise from the fifth block (Sessions 15–16) with those from the final, sixth block, in which the ITIs of the three groups were equated (see Block 6 in Figure 3). An ANOVA with group and block as factors revealed no group differences in responding to the light, $F(2, 42) = 3.1$; there was no effect of block or Group × Block interaction (both Fs < 1). A corresponding analysis on responding to the noise revealed a significant main effect of group, $F(2, 42) = 22.3$, $p < .001$, but no effect of block or Group × Block interaction ($F < 1$). Tukey's post hoc tests conducted on the group main effect indicated that Group L responded at a significantly lower rate than Groups M and S, which did not differ.

The pre-CS rates from the final two-session block were 3.8, 5.3, and 1.3 for Groups M, S, and L, respectively. ANOVA revealed no
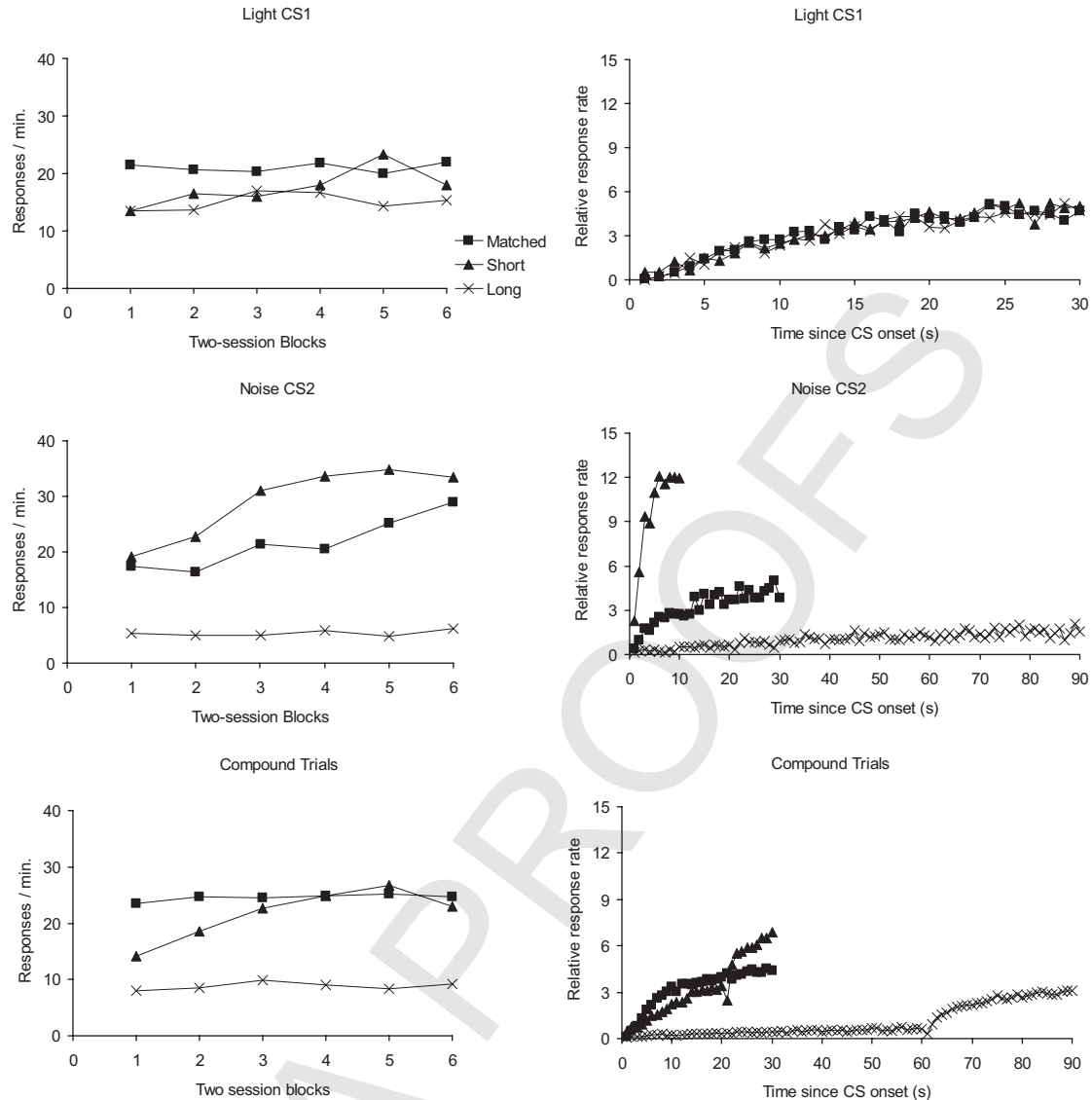
Figure 3. Experiment 3. Left column: The mean rate of responding (responses per minute) to the target stimulus (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel) over five 2-session blocks. Right column: The relative rate of responding as a percentage of the total responses over stimulus duration during reinforced probe trials of the target (top panel), the overshadowing stimulus (middle panel), and the compound stimuli (bottom panel). CS = conditioned stimulus.

effect of group, $F(2, 21) = 2.5$; the results of this test appear to justify the conclusion that the measures of conditioning to the noise and light were not contaminated by differences in background responding.

Compound Trials

The pattern of responding during the training sessions was similar to that observed in Experiments 1 and 2 (bottom left panel of Figure 3). The rate of responding increased in Groups M and S over training but remained relatively stable in Group L. Furthermore, there was an increase in responding from stimulus onset to

food delivery, consistent with the rats having learned the time of food arrival (bottom right panel of Figure 3).

Discussion

Rate expectancy theory proposes that the speed of acquisition is based on a comparison between the rate of reinforcement in the CS and the rate in the background (Gibbon & Balsam, 1981; Gallistel & Gibbon, 2000), which may also affect the asymptote of conditioned responding (e.g., Domjan, 1980; Gibbon et al, 1977; Kirkpatrick & Church, 2000; Lattal, 1999; Salafia et al., 1975; although see Holland, 2000). The present experiment sought to investigate

whether the influence of the C/T ratio could explain our results. The central finding is that matching the C/T ratio for the noise stimulus, as opposed to the light stimulus, did not have a discernible effect on the pattern of results. As in Experiments 1 and 2, little difference was seen in responding to the light as a function of the relative duration of the overshadowing stimulus. Conversely, differences were seen in responding to the noise, and these persisted despite training in which the C/T ratio for this stimulus was equated. With these training parameters, it appears that C/T ratio is not the sole determinant of the rate of conditioned responding. Rather, it is apparent that responding was controlled by the absolute duration of the stimulus. Several studies have demonstrated the importance of absolute duration in different conditioning paradigms (e.g., delay conditioning; Holland, 2000; Kirkpatrick & Church, 2000; partial reinforcement; Bouton & Sunsay, 2003). The present studies extend these effects to overshadowing.

General Discussion

The results of the present experiments yield two major findings. First, overshadowing was unaffected by stimulus duration, regardless of whether the overshadowing stimulus was longer than, shorter than, or of the same duration as the target stimulus. This finding was observed irrespective of the absolute difference in duration between the two CSs and despite the marked differences in responding to the overshadowing stimulus, with shorter stimuli supporting higher rates of responding (Experiments 1 and 2). These results could not be explained by the C/T ratios of the various stimuli. A similar pattern of results was observed in all three experiments, despite the fact that in Experiments 1 and 2 the C/T ratios of the light in the various groups were very similar, whereas those of the noise were not, while in Experiment 3 this relationship was reversed. It is not immediately clear why the present results differ from those of other studies investigating this issue (e.g., Egger & Miller, 1962; Kehoe, 1983), although one possible candidate might be that the present experiments employed stimulus durations that were substantially longer than those used in this previous work. Moreover, as noted in the introduction, our experiments controlled the duration of the target stimulus, so that the effects we observed were not contaminated by differences in response rate produced by differences in target stimulus duration.

Second, although overshadowing was apparent in all groups, there was no corresponding attenuation of timing of the target stimulus. Both experimental and control groups timed the duration of the target stimulus with a similar degree of accuracy. Furthermore, the three experimental groups also displayed accurate timing of the overshadowing noise stimulus.

The simplest account of overshadowing is probably in terms of generalization decrement (Hull, 1943; Rescorla, 1972). When two stimuli are trained in compound, presenting one alone results in its being perceived slightly differently from the way that it is perceived in training. This results in an attenuation of conditioned responding, because the stimulus elements that were present during conditioning are not the same as during the test. Such an account might predict that responding to the target should have been attenuated more in Groups M and L, which had never experienced the light in isolation, than in Group S, which had. However, this was not the case; the experiments reported above

demonstrate that overshadowing did not differ in Groups S, M, and L.

An alternative explanation of overshadowing is in terms of stimulus competition for associative strength. For example, the Rescorla–Wagner model (Rescorla & Wagner, 1972) predicts that when the conditioned response to the overshadowing stimulus is greater than the conditioned response to the target stimulus, there should be a greater overshadowing effect observed relative to the condition in which the conditioned response to the overshadowing stimulus is less than to the target stimulus. This was clearly not the case in the present experiments; we found significantly greater levels of conditioned responding to the noise in Group S than in Groups M and L, yet we observed no differences in overshadowing.

The Rescorla–Wagner model as originally formulated does not possess any means of conceptualizing the effects of stimulus duration with regard to the results presented above. Thus, a more likely explanation of our results might be found in models that do, such as the TD model (Sutton & Barto, 1990) and the time-of-arrival hypothesis (Goddard & Jenkins, 1988). As we noted above, the models make differing predictions about the results of the present experiments. The time-of-arrival hypothesis predicts that a shorter stimulus will produce superior overshadowing because there is less error in estimating shorter durations. This prediction was clearly not borne out in the present experiments. In contrast, the TD model predicts that the longer stimulus will produce superior overshadowing. According to the TD model, each stimulus consists of a series of units that are independently conditioned by a modification of the Rescorla–Wagner model learning rules (Rescorla & Wagner, 1972). However, competition occurs among component units of the CSs rather than between different components of a compound CS. The TD model thus explains overshadowing of two coextensive stimuli in essentially the same manner as the Rescorla–Wagner model. Timing is modeled through variations in the associative strength of CS elements over the course of the CS, with later elements acquiring greater strength. Thus, if one were to make the simple assumption that, compared to the case in which a CS is conditioned alone, in an overshadowing procedure the associative strength of each of the CS elements is halved, then the model could predict lower rates of responding to the target stimulus yet still observe accurate timing of the stimuli. This is because the proportion of the total strength possessed by each element would be the same in both cases.
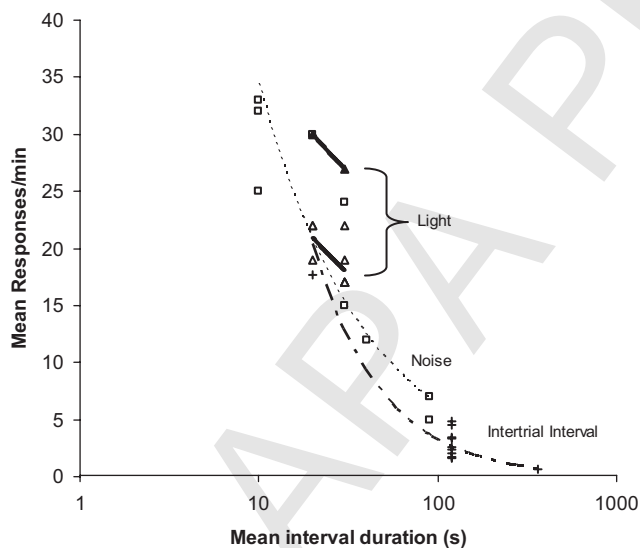
The second reason for conducting these experiments was to establish whether timing of the target CS would be attenuated by the overshadowing CS. There are only a limited number of studies that have directly investigated the interaction between cue competition and timing (e.g., Gaioni, 1982; Jennings & Kirkpatrick, 2006). For example, in the Jennings and Kirkpatrick study, the rats' ability to time the target stimulus was largely unaffected by whether it was subject to blocking. The present results accord with these findings in showing no sign that overshadowing diminished the animals' ability to time the target CS.

Another noteworthy aspect of our results is the large effects of stimulus duration on conditioned responding. Although such differences are routinely found (e.g., Kirkpatrick & Church, 2000; Lattal, 1999), they are usually explained by the argument that the ratio of the reinforcement rate during the background (food–food interval) to the rate of reinforcement during the CS (CS onset–food

interval) is a critical determinant of the level of conditioned responding (e.g., Domjan, 1980). However, in the present experiments, these differences persisted even when the C/T ratio was dramatically altered. For example, responding to the light in the three overshadowing groups remained the same regardless of whether their C/T ratios differed. It appears that absolute stimulus duration was the main determinant of the level of conditioned responding.

This effect of interval duration on responding is shown in Figure 4. Separate functions are plotted for different types of cues across the three experiments, with each data point representing a different group mean. The ITI function shows the effect of ITI duration on pre-CS rates; the noise function shows the effect of noise duration on response rate during noise-only probes. The light functions demonstrate the effect of light duration on responding during light-only probes by experimental (unfilled triangles) and control (filled triangles) groups. Interval duration was a strong predictor of response rates during the ITI, noise, and light cues, and the general relationship was similar in all cases—a decreasing power function (see Kirkpatrick & Church, 2000, 2003, 2004 for similar results). This function form is exactly predicted by packet theory (Kirkpatrick, 2002). The effect of overshadowing on responding to the light appeared to be an additive effect on top of the effect of interval duration, as the slopes of the two light functions were similar (experimental groups: -0.36; control groups: -0.26), indicating a lack of interaction of the two effects. However, this conclusion should be treated with some caution given the limited range of light durations employed in the present research. In any

event, the similar function form for all types of cues lends further support to the notion that temporal factors on responding were independent of the overshadowing that occurred.

In summary, overshadowing occurred regardless of stimulus duration. There were two temporal effects on responding: absolute duration controlled mean response rate, and also the timing of responding. Although there has been much recent focus on integration of timing and conditioning, a seemingly worthy cause, the present results appear to point to a degree of independence in timing and conditioning in overshadowing. The overshadowing results could be predicted by a basic associative model, such as the Rescorla–Wagner model (Rescorla & Wagner, 1972), and the timing results could be predicted by a time-sensitive model of conditioning, such as packet theory (Kirkpatrick, 2002) or the TD model (Sutton & Barto, 1990). However, one should not dismiss the importance of developing successful integrative theories of timing and conditioning on the basis of these results, as there are other paradigms in which these two forms of learning appear to interact (see, e.g., Goddard & Jenkins, 1988).

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Figure 4. The relationship between mean interval duration and the mean rate of responding for different types of intervals: the intertrial interval versus pre-conditioned stimulus rates, the noise duration versus noise probe response rates, and the light duration versus light probe response rates (the light response is separated into experimental [unfilled triangles] and control [filled triangles] groups to display the additive effect of overshadowing treatment on the rate of responding). Each data point represents a group mean for different conditions. The horizontal axis is scaled logarithmically. The smooth line through each set of data points is the best fitting power function.

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AQ1: Have I correctly inserted "unfilled triangles" and "filled triangles" in the Figure 4 caption? Please also define the plus symbols. Please note that a figure should be understandable separate from the text (and all symbols should be defined in the caption).