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Overshadowing by fixed and variable duration stimuli

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Abstract

Two experiments investigated the effect of the temporal distribution form of a stimulus on its ability to produce an overshadowing effect. The overshadowing stimuli were either of the same duration on every trial, or of a variable duration drawn from an exponential distribution with the same mean duration as that of the fixed stimulus. Both experiments provided evidence that a variable duration stimulus was less effective than a fixed duration cue at overshadowing conditioning to a target CS; moreover, this effect was independent of whether the overshadowed CS was fixed or variable. The findings presented here are consistent with the idea that the strength of the association between CS and US is, in part, determined by the temporal distribution form of the CS. These results are discussed in terms of time-accumulation and trial-based theories of conditioning and timing.

Keywords: rats, timing, overshadowing, associative learning, stimulus distribution form

Introduction

When a conditioned stimulus (CS) is reliably followed by an unconditioned stimulus (US), a conditioned response (CR) develops during the CS indicating that the US is anticipated. This change in behaviour has been attributed to the formation of an *association* between the mental representations of these two events, such that presentation of the CS can activate the representation of the US and hence elicit the CR (e.g. Mackintosh, 1975; Pearce & Hall, 1980; Pearce, 1994; Rescorla & Wagner, 1972; Wagner, 1981). Associations are assumed to arise from contiguity between CS and US, but the extent to which an association is strengthened by CS/US pairings is moderated by other factors. This is illustrated by the phenomenon of *cue competition*, of which *overshadowing* is one example.

Associative Accounts of Overshadowing

Cue competition refers to situations in which CS/US contiguity produces varying degrees of conditioning because other cues that are present can effectively compete with the target CS for associative strength. It has been recognised as a critical feature of the associative process, as it selectively promotes learning about events that are positively correlated - and hence likely to be causally related. As the primary aim of the associative theories mentioned above is to delineate the conditions under which associations form, all offer an explanation of cue competition effects.

Perhaps the simplest example of cue competition is *overshadowing*, which refers to the attenuation of conditioned responding that arises if a CS is conditioned in compound with some other cue, rather than being conditioned alone. For example, according to both Rescorla & Wagner (1972) and Pearce & Hall (1980) CS/US contiguity fails to produce conditioning when

the US is fully predicted[1], and the total associative strength that may condition to a given US is limited; thus the more associative strength is acquired by the overshadowing stimulus, the greater an overshadowing effect it will produce. Mackintosh's mechanism is slightly more complex, only predicting overshadowing if the overshadowing stimulus conditions more than the target CS on the first trial. Nonetheless, if overshadowing occurs then this model also predicts that it will increase with the associative strength of the overshadowing stimulus (see also Wagner, 1981).

Associative Models and Time

These associative models rely on the occurrence of *trials*, during which a CS is presented which may or may not be paired with a US. A trial is a potential learning experience for the subject that does not refer to the duration of the constituent events, and so conveniently allows the same description of learning to be applied to CSs and USs that are msec or minutes in duration. Associative models of this type have thus been referred to as *trial-based* (cf. Bouton & Sunsay, 2003), and can be distinguished from alternative associative accounts that stress a more performance-focused approach, and explain cue competition as a *retrieval* deficit (e.g. comparator theory: Denniston, Savastano & Miller, 2001), and from those employ associations as an explanatory tool, but for which associations are not the primary focus (e.g., packet theory: Kirkpatrick, 2002).

Trial-based theories have tended to ignore the effects of temporal factors on the conditioning process, and suppose that properties of the CS such as its duration do not affect the course of learning. Such theories also typically take the magnitude or rate of the CR *computed*

[1] according to Rescorla & Wagner this failure of learning is mediated via a reduction in US processing, according to Pearce and Hall via a reduction in CS processing.

over the entire CS (typically expressed as responses per minute for purposes of comparison) as the primary measure of learning, ignoring variations in the CR at different points of the CS with different proximity to US delivery. Yet the importance of time in conditioning has been recognized since Pavlov (1927), who observed that maximum conditioned responding occurs at the end of temporally extended CSs - *inhibition of delay*. Others have reported a systematic relationship between the relative durations of the CS and intertrial interval (ITI), and both the speed with which the CR develops (Gibbon, Baldock, Locurto and Terrace, 1977) and its final asymptotic rate (e.g. Lattal, 1999; Terrace, Gibbon, Farrell & Baldock, 1975; but see Holland, 2000; Kirkpatrick & Church, 2000). Moreover, in the *peak procedure* a CS conditioned at a fixed duration is tested on longer, peak trials, on which the rate of the CR increases gradually until the point of US delivery and then declines again - suggesting that animals can *time* US occurrence.

More recent work has explored both the degree to which the lawful relationships between CS and ITI durations and the CR may be explained in terms of trial-based theories, and the effect of other temporal factors on conditioning within a trial-based associative framework (e.g., Holland, 2000; Bouton & Sunsay, 2003). Others have used trial-based associative theories as a starting point for development of real-time accounts that explicitly propose how associations can convey temporal information, by regarding each trial as a series of real-time learning episodes (e.g., Kutlu & Schmajuk, 2012; Sutton & Barto, 1987; Vogel, Brandon & Wagner, 2002).[2]

Non-Associative Accounts of Conditioning: Time-Accumulation Models

A different approach to this issue has led to the development of conditioning accounts

[2] These models are more accurately described as episode-based rather than trial-based, but share with trial-based models the assumption that learning occurs incrementally on discrete learning episodes.

which assume that temporal features of the conditioning episode are *central* to what is learned, arguing that information about the temporal properties of the environment extant during learning is obtained by *accumulating* information over a broad temporal window, such as an experimental session (e.g. Gibbon & Balsam, 1981; Gallistel & Gibbon, 2000; see also Balsam & Gallistel, 2009; Balsam, Drew & Gallistel, 2010). Information about the rate of US delivery during the CS, and also in the CS's absence, is computed, and the comparison between these two values indicates the likelihood that the CS signals the US. Once this comparison reaches a certain threshold, a decision is made to respond. This approach rejects the importance of CS/US contiguity (e.g. Balsam & Gallistel, 2009), asserting that the decision to respond depends on information accumulated over a number of trials (although the temporal window over which this accumulation takes place is typically unspecified). Thus, in contrast to the view of the trial-based models outlined above, the trial-by-trial properties of a conditioning episode are not critical to development of the CR. Such theories have been termed *time-accumulation* models (cf. Bouton & Sunsay, 2003).

Time-accumulation models can explain the orderly relationship between conditioned responding and CS and ITI durations, because of the inverse relation between interval duration and reinforcement rate. They are also integrated with an independent timing mechanism (Gibbon, Church & Meck, 1984), comprising a pacemaker from which pulses may be transferred to a short term memory store (STS) via a switch; at CS onset the switch starts diverting pulses into the STS until US delivery, when the stored value is transferred into long term memory. The accumulating pulses in the STS are compared with the values stored in long term memory; once these values are sufficiently close the decision is made to respond. Thus, although on each trial there is an abrupt transition from low to high responding, there is trial-to-trial variability in when

this occurs because of inherent variability in both timing and memory systems (Gibbon et al. 1984). Thus, when averaged over many trials, these models can predict that the CR to a fixed duration CS increases *gradually* until the point at which the US is delivered.

Time-Accumulation accounts of Cue Competition

Time-accumulation models thus provide an integrated explanation of conditioning and timing, leading some to argue that they should supersede trial-based associative theories, which provide neither a principled account of timing, nor quantitative predictions about the effect of temporal factors on acquisition and rate of the CR (e.g., Church & Broadbent, 1990; Kirkpatrick & Church, 1998; although see e.g. Vogel, Brandon & Wagner, 2002; Sutton & Barto, 1987). However, time-accumulation accounts have difficulty explaining cue competition effects like overshadowing. RET, for example, appeals to a decision rule dictating that the CR is elicited *only* by the more salient CS; the fact that overshadowing often appears to be incomplete is attributed to an averaging artefact (e.g. Balsam & Gallistel, 2009; Gallistel & Gibbon 2000). But this view runs contrary to much of the available empirical evidence, which suggests that overshadowing is a graded effect even in individual subjects (e.g. Kehoe, 1982; Thein, Westbrook & Harris, 2008) - a result which follows directly from the error-correction learning rule employed by trial-based associative models (e.g. Rescorla & Wagner, 1971).

Discriminating Trial-Based and Time-Accumulation Accounts

One way of discriminating between trial-based and time-accumulation approaches is to explore the extent to which the characteristics of individual trials affect acquisition of the CR. Time-accumulation models anticipate that in a simple conditioning procedure, as long as mean

ITI and mean CS durations are equated, CR acquisition should be identical. Thus acquisition of the CR to CSs that are either of a fixed duration, or vary in duration from trial to trial but have the same overall mean duration as the fixed CS, should be the same. However, Jennings et al. (2013) reported a higher level of CR to a fixed than to a variable CS - a difference which persisted even when animals were tested under identical conditions.[3] Jennings et al. (2013) interpreted these findings as evidence that the fixed duration CS had acquired more associative strength than the variable CS.

As trial-based associative models by definition assume that learning occurs on a trial-by-trial basis, they have the theoretical apparatus to explain this result, provided assumptions about how the temporal properties of the CS may be conceptualised are added. For example, assume that each CS comprise a sequence of smaller elements, and that the mean duration of both fixed and variable CSs is 2 units: thus the fixed CS is 2 units on every trial, but the variable is equally likely to be 1, 2 or 3 units. Also assume for simplicity that only the final unit, contingent with the US, acquires associative strength. In the fixed case, only unit 2 acquires associative strength, and as it is contingent with the US on every trial it will reach asymptote. However, units 1, 2 and 3 of the variable CS are each contingent with the US on only some trials: specifically, unit 1 on 33% of trials and nonreinforced on 66%, unit 2 will be reinforced on 33% and nonreinforced on 33%, and unit 3 reinforced on 33% of trials, and never nonreinforced. This analysis requires additional assumptions about the relative speed of excitatory and inhibitory conditioning, whether or not conditioning to different stimulus elements interacts, how associative strength is computed across the entire CS and so on; but it may perhaps be taken to illustrate how higher levels of

[3] They also demonstrated differences in the *acquisition* of the CR, in the sense defined by time-accumulation accounts.

conditioning to fixed duration CSs could arise within this theoretical framework.

Overshadowing by Fixed and Variable Duration Cues

In summary, there is evidence that a fixed duration CS acquires more associative strength than its variable counterpart (Jennings et al., 2013). This result is consistent with a trial-based approach, but cannot be explained by time-accumulation theories. The present experiments were designed to provide further evidence for this proposal: Jennings et al. (2013) only demonstrated differences in *performance* of the CR to fixed and variable duration CSs; however, it has long been argued that conditioned responding to a CS may not always be the best indicator of its associative strength (e.g. Hull, 1943; cf. Cole, Barnet & Miller, 1995; Rescorla, 1988). Many authors have argued that the ability to interfere with conditioning to other stimuli can serve as an alternative measure of conditioning to a CS (e.g. Rescorla,1988), and so the present experiments adopted this strategy, examining the extent to which fixed and variable CSs can produce overshadowing. As noted above, trial-based associative theories predict that the degree of overshadowing increases with the associative strength of the overshadowing stimulus. It follows that if a fixed CS acquires associative strength more efficiently than a variable cue, then it should produce greater overshadowing. In contrast, time-accumulation models like RET predict that fixed and variable duration stimuli whose mean duration is equated should not differ in associative strength, and so predict no difference in overshadowing on this basis. Moreover, their specific mechanism for cue competition asserts that whether or not overshadowing occurs depends on the cues' relative salience - which is also unaffected by whether the CS is fixed or variable. The first experiment evaluated these predictions.

Experiment 1

Three groups of animals received training with a light CS. The control groups (Group C) were trained with the light alone, while the overshadowing groups were trained with the light in compound with an overshadowing stimulus, a white noise, that was either of fixed or variable duration (Groups Nf and Nv respectively). Each group was further divided, such that for half of each the light was of a fixed duration, and for half it was of a variable duration. Thus Groups Lf, Nf/Lf and Nv/Lf, were trained with a fixed light, and Groups Lv, Nf/Lv and Nv/Lv with a variable duration light. In Groups Nf/Lf and Nv/Lv the noise and light had a common onset and offset, whereas in Groups Nf/Lv and Nv/Lf they had different onsets but a common offset (see Figure 1). We anticipated that overshadowing would occur, resulting in less CR to the light at test in the overshadowing groups than in the control groups. But more critically, we predicted differences among the overshadowing groups - more specifically, if a fixed stimulus overshadows more effectively than a variable CS, there should be less responding to the light in Groups Nf/Lf and Nf/Lv than in Groups Nv/Lf and Nv/Lv.

Figure 1 about here

Methods

Subjects:

Subjects were 24 male Lister hooded rats (Harlan UK) with a mean free-feeding weight of 290 g (range: 275-315 g). The rats were weighed daily, and their daily food ration restricted such that their weights reduced to 85% of free-feeding levels before the start of the study. They were

maintained at this level throughout training, their 85% level being adjusted weekly according to a growth curve, so that their weight increased gradually over the course of the experiment. Water was freely available in the home cages. They were maintained on a 12-hour light/dark cycle, with the lights turned on at 7am; temperature was maintained at 21 ˚C (± 1 ˚); the humidity was 60 % (± 10 %). There were 4 animals in each of the six groups (8 per experimental condition).

Apparatus

All conditioning and testing procedures were conducted in eight identical chambers (20 x 24 x 30 cm). Each was situated in a ventilated, noise-attenuating box (74 x 38 x 60 cm) (MED Associates), and equipped with a speaker for delivering auditory stimuli, a houselight, a foodcup and two jewel lights, one situated on each side of the food cup. The houselight was not employed. A speaker, located on the right side of the wall of the chamber opposite the food cup, could deliver a 74-dB (scale A, measured near the food cup) white noise. A 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 recorded by breaking an infra-red photobeam and recorded as a response. Med-PC for Windows (Tatham & Zurn, 1989) controlled experimental events.

Procedure:

Training: All animals received four sessions of training, each comprising 40 trials in which the light was reinforced. In Groups Lf and Lv the light was presented in isolation, while in the remaining groups the noise was also present; for Groups Nf/Lf and Nf/Lv the noise was a fixed 15 s in duration whereas in Groups Nv/Lf and Nv/Lv the noise was of a variable duration with a mean of 15 s. In addition in Groups Lf, Nf/Lf and Nv/Lf the light was of a fixed 15-s

duration, while for Groups Lv, Nf/Lv and Nv/Lv the light was variable, again with a mean duration of 15 s; the variable durations were drawn from an exponential distribution with an arithmetic mean of 15 s. In Groups Nf/Lf and Nv/Lv the noise and light were coextensive, whereas in Groups Nf/Lv and Nv/Lf the noise always ended at the same time as the light, but its onset either preceded or followed that of the light (see Figure 1). Each trial comprised the CS presentation, and also a 15-s preCS period that immediately preceded onset of the CS (when the noise and light were asynchronous the preCS period immediately preceded whichever of these stimuli started first); light offset was immediately followed by the delivery of a food pellet on all trials. Each trial was separated by an intertrial interval (ITI) comprising a fixed interval of 60 s plus an additional variable period with a mean duration of 60 s; this resulted in an average ITI duration of 120 s.

Testing: The testing phase was identical to the training phase, except that there were 30 rather than 40 of the reinforced trials described in the previous section. The remaining trials in the session were nonreinforced test trials, which were all of a fixed 15-s duration. All six groups received 5 test trials with the light presented alone, which allowed us to evaluate the extent of the overshadowing effect. In addition the four overshadowing groups received five nonreinforced 15-s presentations of the noise/light compound, which were used as a baseline against which overshadowing could be assessed (see below). Thus Groups Lf and Lv received 35 trials in each test session, and Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv 40 trials. The different types of trial were presented in a semi-random order, with the constraint that every six compound trials was presented in a block with one noise/light and one light test trial for the overshadowing groups, and with one light test trial for the control group. There were two sessions in this stage.

Data analysis:

Training: The time of occurrence of each stimulus onset, stimulus termination, food delivery, and head entry response was recorded with a resolution of 10 ms. To assess conditioning a *corrected* score was employed. This was obtained by computing the mean response rate during each type of trial in each session, and subtracting the mean response rate from the preCS periods in that session. In Groups Nv/Lf and Nf/Lv, noise and light were not coextensive. Thus, so that responding could be evaluated under the same stimulus conditions in all four overshadowing groups, data are reported only during the time interval when both stimuli were being presented (which was on average shorter than 15 s).

To confirm that the baseline preCS rates from which the corrected scores were derived did not differ (as differences would compromise interpretation of the corrected response rates) a corresponding analysis of preCS rates was also conducted.

Test: The test data were pooled across both test sessions. The degree to which conditioning to the light was overshadowed by examining

(i) corrected rates of responding on light test trials, and

(ii) an overshadowing ratio. The ratio was intended as a better control for between-subject variability than correcting for preCS responding, as preCS response rates were close to floor. The overshadowing ratio took the form $a/(a+b)$, where a was the uncorrected response rate during the light test trials, and b the uncorrected rate on the noise/light test trials; these rates were pooled over both test sessions. We employed uncorrected rates to ensure a and b were both positive values, as negative values would render the ratio uninterpretable. This ratio gave a measure of the proportion of responding on training trials that was attributable to the light. If there was no

overshadowing, and the light acquired all the associative strength, then responding on trials with the noise/light compound would be identical to responding on test trials with the light alone. Thus the values of *a* and *b* would be the same, and the value of $a/(a+b)$ approximate 0.5; but as overshadowing increased, the proportion of responding to the noise/light compound that could be attributed to the light would fall, and the ratio would drop below 0.5.

In each case analysis was also performed on the baseline scores from which these two measures were derived - preCS response rates for (i) and uncorrected response rates during the noise/light test trials for (ii).

Timing of the Noise: Timing of the noise was also evaluated, to confirm that the animals were sensitive to the different temporal properties of the fixed and variable duration overshadowing stimuli. The number of responses occurring in successive 1-s time bins of the noise CS was determined in a specific session or group of sessions, and the rate of responding in each bin calculated for each rat. For the variable CS the computation of response rate took into account the number of trials on which the CS was actually present in each time bin. These response rate functions were then normalized so that each rat contributed equally to the shape of the functions regardless of its overall response rate. Thus the response rate in each time bin was divided by the summed response rate and multiplied by 100, giving the percentage of total responses in each time bin for each subject. Then a linear function was fitted to each normalised response rate function, and the slope determined from the best-fitting linear curve for each rat (linear fits provide a good characterisation of the response rate function: Jennings et al. 2007; cf. Kirkpatrick & Church 2000). The temporal slopes were compared against a mean of zero using one-sample t-tests; significance was assessed after applying the Bonferroni correction to the

presented *p* value. In Experiment 1 timing data for the noise CS were derived from responding during the noise in the compound trials of the final training session, pooled for the two groups trained with a fixed duration noise, Nf/Lf and Nf/Lv, and also for the two groups trained with a variable noise, Nv/Lf and Nv/Lv

A significance level of $p < .05$ was adopted throughout. All data were analysed using ANOVA with overshadowing CS (noise absent, fixed or variable) and target CS (light fixed or variable) as between-subjects factors and session as within-subjects factor; significant two-way interactions were examined with simple main effects analysis, using the pooled error term. Main effects of overshadowing CS were examined using Tukeys HSD test. *MSE*s and *p* values are presented for all *Fs* greater than 1, and partial η^2 (a measure of effect size) is given for all significant main effects and interactions.

Results

Figure 2 here

Conditioned responding:

Training: All six groups rapidly acquired conditioned responding (see Figure 2). It should be noted that it is difficult to draw firm conclusions from the compound training phase. Not only did different groups experience different physical stimuli, but also in Groups Nf/Lv and Nv/Lf, for which one of the CSs was fixed and the other variable, the period for which they overlapped would have been on average shorter than 15s. As a consequence response rates during the noise/light compound in these groups would not be strictly comparable to those in Groups Nf/Lf

and Nv/Lv, for whom the average recording period on each trial would have been 15s.

ANOVA performed on the corrected scores, with overshadowing CS (noise absent, fixed or variable), target CS (light fixed or variable), and session as factors revealed a significant three-way interaction, $F(6, 54) = 4.76$, $p < .001$, $MSE = 14.24$, partial $\eta^2 = .35$; there was also an interaction between session and overshadowing CS, $F(6, 54) = 3.60$, $p = .004$, $MSE = 14.24$, partial $\eta^2 = .29$, and significant effects of target, overshadowing CS and session, $F(1, 18) = 5.41$, $p = 032$, $MSE = 31.18$, partial $\eta^2 = .23$; $F(2, 18) = 5.86$, $p = .011$, $MSE = 31.18$, partial $\eta^2 = .39$; and $F(3, 54) = 99.71$, $p < .001$, $MSE = 14.24$, partial $\eta^2 = .85$ respectively. Nothing else was significant, largest $F(2, 18) = 3.18$, $p = .066$, $MSE = 31.18$. To examine the three-way interaction, separate ANOVAs were conducted on the data from the three groups for each target CS condition (light fixed or variable), with overshadowing CS and session as factors. For the groups trained with a fixed duration light this revealed only a significant effect of sessions, $F(3, 27) = 55.1$, $p < .001$, $MSE = 12.75$, partial $\eta^2 =. 86$; the effect of overshadowing CS and the interaction were not significant, $F < 1$ and $F(6, 27) = 2.07$, $p = .09$, $MSE = 12.75$ respectively. The corresponding analysis of the data from the groups trained with a variable CS revealed a significant interaction, $F(6, 27) = 5.89$, $p < .001$, $MSE = 15.73$, partial $\eta^2 = .57$. The three overshadowing CS conditions differed on sessions 2, 3 and 4, smallest $F(2, 36) = 4.77$, $p = .015$, $MSE = 18.01$ for session 3MSE; Tukeys tests revealed that Group Nf/Lv responded more than Group Lv on sessions 2 and 3, $p < .01$ and .05 respectively, and Group Nv/Lv less than Groups Lv and Nf/Lv on session 4, $p < .05$ and .01 respectively; in addition Group Lv responded less than Group Nv/Lv on session 2, $p < .05$. Thus when the target light was fixed all three groups appear to acquire the CR at similar rates, but differences were evident when the target CS was variable, the most consistent of these being the relatively higher response rates in Group Nf/Lv.

The group mean preCS scores for sessions 1-4 are shown in Table 1. ANOVA with target CS, overshadowing CS and sessions as factors revealed a main effect of target CS, $F(1, 18) = 5.16$, $p = .036$, $MSE = 9.21$, partial $\eta^2 = .22$; background responding was slightly but consistently higher in animals trained with a variable light (Lv, Nf/Lv and Nv/Lv). It is possible that the higher response rates seen in groups trained with the variable light indicates less effective overshadowing of the context by this stimulus. There was also a main effect of overshadowing CS, $F(2, 18) = 3.75$, $p = .043$, $MSE = 9.20$, partial $\eta^2 = .29$ respectively, which interacted significantly with sessions, $F(6, 54) = 3.90$, $p = .003$, $MSE = 4.26$, partial $\eta^2 = .30$; simple main effects revealed an effect of overshadowing CS on sessions 3 and 4, $F(2,72) = 9.84$, $p = .0002$, and $F(2,72) = 3.48$, $p = .036$, $MSE = 5.49$ for sessions 3 and 4 respectively, and Tukeys test showed that in session 3 the control groups responded more than both fixed and variable groups, $p < .01$ and $p < .05$ respectively, while on session 4 the fixed groups responded more than the variable groups, $p < .01$. There was also a significant effect of sessions, $F(3, 54) = 29.5$, $p < .001$, $MSE = 4.26$, partial $\eta^2 = .62$, but nothing else was significant, largest $F(3, 54) = 1.44$, $p = .24$, $MSE = 4.26$.

Finally, the mean duration of the variable noise over these four training sessions was 14.05s (sem = 2.16s); these values did not differ from the target value of 15s on any session.

Test: All the test trials were of a fixed 15-s in duration.

Light: Corrected scores: The mean corrected rates of responding to the light are shown in the top panel of Figure 3. Responding to the light was clearly lower in the overshadowing than in the control groups, suggesting that overshadowing had occurred - but it was less clear that the

overshadowing effect differed among the groups: although responding was numerically greater in Group Nf/Lf than in Group Nv/Lf, responding in Groups Nf/Lv and Nv/Lv was very similar. ANOVA confirmed this description of the data, revealing a significant main effect of overshadowing CS, $F(2, 18) = 22.25$, $p < .001$, $MSE = 25.70$, partial $\eta^2 = .71$; nothing else was significant, $Fs < 1$. However, Tukeys test revealed that although responding to the light was significantly higher in the control groups than in both overshadowing groups $ps < .01$, responding to the light in the overshadowing groups did not differ. Thus there was evidence that overshadowing had occurred, but not that it differed in magnitude among the various conditions on this measure.

The mean preCS rates, pooled over all trial types, were 3.86, 1.21 and 1.23 rpm for Groups Lf, Nf/Lf and Nv/Lf, and 4.79, 1.11 and 4.86 rpm for Groups Lv, Nf/Lv and Nv/Lv. respectively. ANOVA revealed main effects of target CS, again indicating higher rates of background responding when the light was variable, $F(1, 18) = 6.06$, $p = .02$, $MSE = .219$, partial $\eta^2 = .25$, and of overshadowing CS, $F(2, 18) = 9.26$, $p = .002$, $MSE = .219$, partial $\eta^2 = .51$; the interaction was not significant, $F(2, 18) = 3.39$, $p = .06$, $MSE = .219$. Tukeys test revealed preCS rates were higher in the control than in the fixed groups, $p = .01$.

Figure 3 here

Light: Overshadowing Ratio:

To examine differences *among* the overshadowing groups in a more sensitive manner, an overshadowing ratio was calculated using the mean uncorrected rates of responding on the noise/light test trials as a baseline. The resultant ratios are shown in the lower panel of Figure 3, and it is clear that overshadowing ratios were lower in Groups Nf/Lf and Nf/Lv than Groups

Nv/Lf and Nv/Lv, an effect which was independent of the temporal distribution of the light. This pattern is consistent with the prediction that overshadowing would greater in groups trained with a fixed duration noise. ANOVA with overshadowing CS (noise fixed or variable) and target CS (light fixed or variable) as factors confirmed that there was a main effect of overshadowing CS, $F(1, 12) = 5.41$, $p < .04$, $MSE = .007$, partial $\eta^2 = .31$, but no effect of target or interaction, $Fs < 1$. Thus the overshadowing ratios demonstrated a significantly greater overshadowing effect when the overshadowing stimulus was fixed than when it was variable.

The uncorrected rates of responding during the noise/light test trials scores 23.4, 25.3, 20 and 20.7 rpm for Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv respectively and did not differ - ANOVA with overshadowing CS and target revealed nothing significant, largest $F(1, 12) = 1.57$, $p = .24$, $MSE = 40.89$.

Figure 4 here

Timing of the Noise: The mean response rates in each 3-s bin of the final training session were collapsed over the two groups trained with a fixed noise, Nf/Lf and Nf/Lv, and those trained with a variable noise, Nv/Lf and Nv/Lv; the resulting data are presented in Figure 4. There appeared to be a gradual increase of responding over the course of the CS in the groups trained with a fixed noise, but not in those trained with a variable noise. ANOVA with overshadowing CS (fixed or variable) and bin as factors revealed no effect of overshadowing CS, $F < 1$, but a significant effect of bin $F(4, 56) = 12.08$, $p < .001$, $MSE = 33.11$, partial $\eta^2 = .46$, and a significant interaction between these two factors, $F(4, 56) = 5.28$, $p = .001$, $MSE = 33.11$, partial $\eta^2 = .27$; however responding in the two overshadowing CS conditions did not differ on any bin,

largest $F(1, 70) = 3.34$, $p = .073$, $MSE = 66.16$ for bin 4. There was also a significant effect of bin for the fixed, $F(4, 56) = 16.03$, $p < .001$, $MSE = 33.11$, but not the variable overshadowing CS condition, $F(4, 56) = 1.33$, $p = .27$, $MSE = 33.11$. The mean slope for the fixed and variable conditions was .61 and .16 respectively, and these scores differed significantly, $F(1, 15) = 7.54$, $p = .016$, $MSE = .35$, partial $\eta^2 = .35$; the former value differed significantly from zero, $p < .001$, but the latter did not, $p = .233$. This suggests that the animals showed patterns of responding over the noise CSs appropriate to their temporal distributions (cf. Kirkpatrick & Church, 1998).

Discussion

The results of this experiment suggest that a fixed stimulus overshadows more effectively than a variable one: conditioned responding on the light test trials in Groups Nf/Lf and Nf/Lv represented a lower proportion of responding during the noise/light compound than in Groups Nv/Lf and Nv/Lv; however, this difference was not evident in the corrected response rates to the light in the present experiment. Nonetheless, the difference in the overshadowing ratios is consistent with the suggestion that, although of the same mean duration, fixed duration CSs condition better than cues whose duration varies from trial to trial (Jennings et al., 2013).

Moreover, these findings rule out some potential alternative explanations. For example, Miller and colleagues proposed the temporal coding hypothesis (e.g. Blaisdell, Denniston & Miller, 1998), according to which the temporal relationship between the two events that are associated during a conditioning procedure is automatically encoded as part of the association, and affects what may be learned. Although this theory does not fall into the class of trial-based associative models we set out to test, it predicts that cue competition will be maximal when both

cues convey identical temporal information. Blaisdell et al. confirmed this prediction, demonstrating robust overshadowing *only* when the overshadowing cue had the same temporal relation to the US as the target, where temporal information referred to whether the CSs preceded the US, followed it, or CS and US were coextensive (Blaisdell et al., 1998). If one extends the definition of temporal information to whether the CS is of fixed or variable duration, then the temporal coding hypothesis predicts better overshadowing when both cues are fixed, or both are of the same variable durations (e.g. *both* 5 s on one trial, and 3 s on another). This would predict greater overshadowing in Group Nf/Lf than in Nv/Lf, as we found - but also greater overshadowing in Group Nv/Lv than in Group Nf/Lv, the opposite to what we observed. Thus the present findings cannot be explained in terms of the temporal coding hypothesis.

A second potential explanation of our results appeals to generalisation decrement. In Group Nf/Lf the light was never experienced in the absence of the noise, as the two cues overlapped perfectly, whereas in Group Nv/Lf the light was experienced alone on all trials on which the noise was shorter than 15s. This could result in more generalisation decrement of the light at test in Group Nf/Lf - reducing responding and thus resulting in an apparently stronger overshadowing effect (cf. Kehoe, 1983). However, this account would also predict greater overshadowing in Group Nv/Lv, in which noise and light were coextensive, than in Group Nf/Lv, in which they were not - but the opposite pattern was observed. Thus these results cannot be explained in terms of generalisation decrement (see also Jennings et al. 2007).

One issue with the present study concerns the ratio measure. In principle this technique is no different from the standard practice of correcting for rates of preCS responding, as it merely allows responding during the stimulus of interest to be corrected against a baseline measure of individual differences in response rates. Nonetheless, it would be more compelling if we could

demonstrate our key differences using the less derived corrected response rate measure of responding to the light. Thus in Experiment 2 the intensity of the noise CS was slightly increased, with the hope of exaggerating overshadowing, and thus revealing differences in the response rate measure.

Experiment 2

Experiment 2 was formally identical to Experiment 1, but with a few key differences. First, the intensity of the noise was increased to 75dB. Second, in Experiment 1 we demonstrated differences in the pattern of responding to the fixed and variable duration overshadowing stimuli by examining behaviour to the noise during compound training trials. It would be helpful to have confirmation that animals would show similar behaviour to the noise when presented alone, to rule out the possibility that the pattern we observed was contaminated by the presence of the target light CS. Accordingly Experiment 2 incorporated probe trials with the noise during the training sessions, during which timing could be examined. Third, our account would predict higher response rates to the fixed than to the variable noise (cf. Jennings et al, 2013), but Experiment 1 did not examine responding to this stimulus. Thus in Experiment 2 responding to the noise alone was examined, both in the probe trials just described, and also by adding two sessions of test trials with the noise CS after the test of the light. The first test comprised compound training intermixed with 15-s fixed duration test trials with the noise alone. The second comprised only noise trials, half of fixed duration and the remainder of variable duration, a procedure designed to equate generalisation decrement between the training and test conditions for all animals.

Methods

Subjects:

Subjects were 24 male Lister hooded rats (Harlan UK) with a mean free-feeding weight of 312 g (range: 295-340 g). They were maintained and allocated to groups exactly as in the previous experiment. At the start of deprivation one subject (allocated to Group Lv) was found to be unable to maintain his body weight without special feeding, and so was excluded from the experiment.

Apparatus

The apparatus was identical to that of the previous experiment, except that the intensity of the noise was increased from 74 to 75 dB.

Procedure:

Training: The four training sessions were identical to those of Experiment 1 except for the addition of five, 15-s nonreinforced probe trials with the noise in the four overshadowing groups in each session; trials were arranged in five, 9-trial blocks each comprising eight reinforced compound trials and one probe trial.

Light Test: The first testing phase was identical to that of the previous experiment. There was one session in this stage.

Noise Test: The final two sessions were received only by the four overshadowing groups. The first comprised 25 compound trials, exactly as in the training phase, plus 15 15-s test trials -

presentations of the noise, 10 of which were reinforced and the remaining 5 nonreinforced. These trials were delivered in blocks of 8 trials, 5 compound trials, and two reinforced and one nonreinforced noise trial, delivered in a semi-random order. The second comprised only test trials with the noise: Thus in this final session all animals received 20 15-s fixed and 20 mean 15-s variable duration noise presentations; half of each trial type were followed by food and the remainder were nonreinforced. In all other respects this test session was identical to the previous sessions.

Data Analysis: This was identical to that of Experiment 1, except that timing data were also computed for the noise during the probe trials of the last conditioning sessions. In addition the corrected response rates to the noise in the probe trials of the training sessions, as well as in the two test sessions, were also reported.

Results

Conditioning responding:

Training: Group mean corrected scores from the four training sessions are shown in Figure 5; again there seemed to be evidence of overshadowing in all four overshadowing groups, but this appeared to be more profound in Groups Nf/Lf and Nf/Lv trained with the fixed duration noise. ANOVA with overshadowing CS (absent, fixed or variable), target CS (fixed or variable), and session as factors revealed a significant main effect of session, $F(3, 51) = 96.98$, $p < .001$, $MSE = 16.52$, partial $\eta^2 = .851$, and a significant interaction between overshadowing CS and session, $F(6, 51) = 2.66$, $p = .025$, $MSE = 16.52$, partial $\eta^2 = .24$. Nothing else was significant, largest $F(2, 17) = 2.21$, $p = .14$, $MSE = 41.38$ for the overshadowing CS x target interaction. Exploration

of the significant interaction between overshadowing CS and session revealed only a significant difference between the conditions on session 2, $F(2, 68) = 3.52$, $p = .04$, $MSE = 22.74$, but Tukeys tests did not reveal any differences between the three overshadowing CS conditions; there were no differences on any other session, largest $F(2, 68) = 1.92$, $p = .15$, $MSE = 22.74$ for session 4.

This study also examined response rates to the noise in isolation on the probe trials; the corrected response rates on these trials are shown in top panel of Table 2. Response rates tended to be higher when the noise was fixed, and also when the light was fixed; ANOVA with target CS, overshadowing CS and sessions as factors revealed mean effects of all three, $F(1,12) = 6.37$, $p = .03$, $MSE = 17.42$, partial $\eta^2 = .35$, $F(1,12) = 6.45$, $p = .03$, $MSE = 17.42$, partial $\eta^2 = .35$, and $F(13,36) = 16.23$, $p < .001$, $MSE = 27.72$, partial $\eta^2 = .58$. Nothing else was significant, largest $F(3,36) = 2.37$, $p= .09$, $MSE = 27.72$. Thus, far from the fixed duration noise eliciting more conditioned responding than the variable, the opposite was the case.

Figure 5 here

The group mean preCS scores for sessions 1-4 are shown in the lower panel of Table 1. ANOVA with target CS, overshadowing CS and sessions as factors revealed a main effect of overshadowing CS, $F(2, 17) = 9.45$, $p = .002$, $MSE = 7.23$, partial $\eta^2 = .53$, and also a significant main effect of session, $F(3, 51) = 17.36$, $p < .001$, $MSE = 3.57$, partial $\eta^2 = .51$; nothing else was significant, largest $F(6, 51) = 1.53$, $p = .19$, $MSE = 3.57$. Tukey tests were used to explore the main effect of condition, and revealed that rates of preCS responding were higher in the control than in the fixed condition, $p < .01$.

Finally, the mean duration of the variable noise over these four training sessions was 13.81s (sem = 2.06s); these values did not differ from the target value of 15s on any session.

Figure 6 here

Test:

Light: Corrected scores: The mean corrected rates of responding to the light are shown in the top panel of Figure 6. There was not only a marked overshadowing effect, but it appeared more profound with the fixed overshadowing stimulus. ANOVA with overshadowing CS and target as factors revealed a significant main effect of overshadowing CS, $F(2, 17) = 14.82$, $p < .001$, $MSE = 38.71$, partial $\eta^2 = .635$; nothing else was significant, $Fs < 1$. Tukeys test revealed that responding to the light was significantly lower in the fixed groups than in both the control and the variable conditions $ps < .01$. Thus there was evidence for overshadowing, but only in the fixed condition.

The mean preCS rates during this session were 2.3, 0.4 and 1.2 rpm for Groups Lf, Nf/Lf and Nv/Lf, and 1.7, 0.6 and 1.5 rpm for Groups Lv, Nf/Lv and Nv/Lv respectively. ANOVA revealed only a main effect of overshadowing CS, $F(2, 17) = 4.1$, $p = .04$, $MSE = .97$, partial $\eta^2 = .33$; nothing else was significant, $Fs < 1$. Tukeys test revealed that preCS rates were higher in the control than in the fixed groups, $p < .05$ - although, as in the previous experiment, these differences were extremely small relative to rates of responding during the CS.

Light: Overshadowing Ratio: The overshadowing ratios are shown in the lower panel of Figure 6, where it is evident that greater overshadowing was produced by a fixed than a variable duration light. ANOVA with overshadowing CS and target as factors revealed a significant main

effect of overshadowing CS, $F(1,12) = 9.14$, $p = .01$, $MSE = .016$, partial $\eta^2 = .43$. Thus in the present study this measure yielded the same result as the corrected response rates to the light - greater overshadowing by the fixed duration stimulus.

The mean uncorrected rates of responding during the noise/light test trials, which were used as a baseline for the overshadowing measure, were 18.8, 17.4, 19.4 and 24.6 rpm in Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv respectively, and did not differ - ANOVA with overshadowing CS and target as factors revealed nothing significant, largest $F(1, 12) = 3.26$, $p = .1$, $MSE = 18.63$ for the effect of target CS.

Timing: Training compound trials: The distribution of responding over the course of the noise, computed over five, 3-s bins, during the compound trials of the final training session is shown in Figure 7 (top panel), pooled over Groups Nf/Lf and Nf/Lv, and over Groups Nv/Lf and Nv/Lv. As in Experiment 1, responding appeared to increase gradually over the course of the CS in the fixed groups, but not in the variable groups; there were also slightly higher rates at the end of the CS in the fixed condition. ANOVA with overshadowing CS (fixed or variable) and bin as factors revealed no effect of overshadowing CS, $F(1, 14) = 1.05$, $p = .32$, $MSE = 180.1$, but a significant effect of bin $F(4, 56) = 6.84$, $p < .001$, $MSE = 24.57$, partial $\eta^2 = .33$, and a significant interaction, $F(4, 56) = 10.24$, $p = .001$, $MSE = 24.57$, partial $\eta^2 = .43$; responding in the two overshadowing CS conditions differed significantly in the first bin, $F(1, 70) = 17.4$, $p = .001$, $MSE = 55.68$, although not on any other bin, largest $F(1, 70) = 2.26$, $p = .14$, $MSE = 55.68$ for bin 2. There was also a significant main effect of bin for the fixed but not the variable condition, $F(4, 56) = 16.45$, $p < .001$, $MSE = 24.57$ and $F < 1$ respectively. The mean slope was .58 and -.07 for the fixed and variable conditions respectively, and these scores differed significantly, $F(1,$

15) = 19.31, p = .001, *MSE* = .35, partial η^2 = .35; the former value differed significantly from zero, p < .001, whereas the latter did not, p = .57. Thus animals again clearly timed the noise in the fixed condition.

Timing: *Training Noise Probe Trials:* Responding to the noise alone during the probe trials (averaged across sessions) is shown in Figure 7 (lower panel). ANOVA revealed no effect of overshadowing CS, F<1, but a significant main effect of sessions, F(4,56) = 4.55, p = .003, *MSE* = 33.16 partial η^2 = .25, and also a significant interaction between overshadowing CS and bin, F(4, 56) = 3.73, p = .009, *MSE* = 12.48, partial η^2 = 0.21; the overshadowing CS conditions differed on bin 1, F(1, 70) = 4.89, p = .03, *MSE* = 99, and there was an effect of bins in the fixed but not the variable conditions, F(4,56) = 7.34, p = .0001, *MSE* = 33.16 and F < 1 respectively. The mean slopes for fixed and variable conditions were 0.52 and 0.09 respectively, and differed significantly, F(1, 15) = 14.98, p = .002, *MSE* = .051, partial η^2 = .52; the former differed from zero whereas the latter did not, p < .001 and p = .37 respectively. Thus the pattern of responding on the probe trials was essentially similar to that evident during the compound trials.

Figure 7 about here

Noise Test: No differences in responding to the noise as a function of experimental condition were observed in either test:

Test 1: The mean corrected response rates for the test trials were 12.5, 12.8, 14.8 and 18.9 rpm for Groups Nf/Lf, Nf/Lv and Nv/Lf, Nv/Lv, respectively, and these scores did not differ, largest F(1, 12) = 2.01, p = .18, *MSE* = 35.1. PreCS scores for this session were 0.93, 0.8, 2.1 and 2.6

rpm for Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv respectively; ANOVA revealed a significant main effect of overshadowing CS, $F(1, 12) = 13.88$, $p = .003$, $MSE = .62$, partial $\eta^2 = .54$ indicating higher background responding in the groups trained with a variable noise. Nothing else was significant, $Fs < 1$.

Test 2: The mean corrected response rates are shown in Table 2 (lower panel). Responding was substantially higher on test trials which had a fixed duration, regardless of group: ANOVA with overshadowing CS, target CS and test trial distribution (fixed or variable) revealed a significant effect of test trial distribution, $F(1, 12) = 28.08$, $p < .001$, $MSE = 44.10$, partial $\eta^2 = .70$; nothing else was significant, largest $F(1, 12) = 1.58$, $p = .23$, $MSE = 44.1$. Mean preCS scores were 2.8 3.4, 4.3, and 3.5 rpm for Groups Nf/Lv, Nv/Lv, Nf/Lf and Nv/Lf respectively, and did not differ, $Fs < 1$.

Discussion

The results of this experiment replicate those of Experiment 1 - better overshadowing by fixed than by variable duration cues - with the more direct, response rate measure as well as with the overshadowing ratio employed in Experiment 1. It seems likely that this was due to the increase in noise intensity exaggerating the overshadowing effect in the fixed condition: comparing the lower panels of Figures 3 and 6 suggests that the overshadowing ratios were lower in the present experiment than in Experiment 1. Thus, although the degree of overshadowing in the variable condition was roughly constant, that in the fixed condition appeared to be enhanced, which is consistent with this interpretation.

As in Experiment 1, there was also evidence that by the end of compound training the animals were responding differentially over the course of the fixed and variable duration noise; when the noise was fixed responding increased gradually over the course of the CS, whereas when it was variable responding remained constant as the stimulus progressed. Moreover this pattern was just as evident on the compound trials as on the probe trials with the noise alone, confirming that the presence of the light was not contaminating our observations. The study was less successful in revealing greater levels of conditioned responding to the noise when it was of fixed duration: in neither test was there any evidence for any difference in response rate to the noise according to whether it was of fixed or variable duration during training. Indeed, during the probe trials of the training sessions animals in Groups Nv/Lf and Nv/Lv actually responded more than Groups Nf/Lf and Nf/Lv - although the failure to observe this effect in either test session raises doubts about the reliability of this finding. Nonetheless, our hypothesis would predict higher associative strength during the fixed duration CS, and so at face value the failure to observe this is inconsistent with our suggestion.

There are, nonetheless, a number of potential reasons for this apparent discrepancy. First, our pilot work suggests that the parameters used in these experiments are not conducive to showing the difference in responding to fixed and variable duration cues that was shown by Jennings et al. (2013). We conducted two almost identical experiments very similar to those reported here, using noises of differing intensities. When the noise was of a higher intensity it supported significantly greater conditioned responding when it was of a fixed duration, consistent with our predictions - but overshadowing was too profound for any differences in the level of overshadowing to be detected. In contrast, with a lower intensity noise differences in overshadowing were seen, but differences in responding to the noise were no longer detectable.

Thus it may be that the parameters conducive to observing graded overshadowing are not those best suited to observing differences in conditioning to the overshadowing stimulus. Second, the 15-s duration of the stimuli used here was much shorter than the 30-s or 60-s CSs employed by Jennings et al. (2013). As it is well established that factors other than associative strength, such as arousal and CS intensity, can also influence CR performance (e.g. Hull, 1943), it is possible that, with these shorter stimuli factors other than associative strength, such as the arousal induced by CS onset, have a greater influence on performance than with longer CSs. Indeed, to use overshadowing to obtain a measure of associative strength that did not rely solely on conditioned responding was the rationale underlying the present studies. Considerations of this type could in principle explain the pattern of responding to the noise observed in the present studies - as well as the fact that no clear difference in responding to the fixed and variable duration light was observed in our control groups, which we would also anticipate.

Finally, as noted in the introduction, the explanation of overshadowing offered by RET is that it is all or nothing, and not a graded effect. We took the opportunity to examine the data from the individual animals, in order to evaluate this prediction, we have plotted the overshadowing ratios from the individual animals. These data may be seen in Figure 8, and there is little indication that overshadowing is an all or nothing phenomenon.

Figure 8 about here

General Discussion

In both the experiments reported above a fixed duration stimulus produced more overshadowing than a variable CS with the same mean duration, regardless of the distribution form - fixed or variable - of the overshadowed CS. We noted above that many trial-based theories predict that an overshadowing stimulus that can acquire associative strength more effectively will also produce a more profound overshadowing effect. Thus our findings are consistent with the suggestion that fixed duration stimuli acquire associative strength more effectively than their variable counterparts. In this respect these data are consistent with the findings reported by Jennings et al. (2013) that fixed duration CSs support more conditioned responding - but using a measure of associative strength other that strength of the conditioned response.

Time-accumulation models do not have the theoretical framework to explain differences in acquisition of associative strength by fixed and variable duration cues, as they would regard such stimuli as functionally equivalent if their mean duration is matched. In contrast, trial-based models, despite typically neglecting a conceptualisation of temporal cues, have the theoretical framework to explain effects of this type. One very casual example of how fixed cues might condition better than variable cues was given in the introduction; however, the same prediction can be generated by a trial-based model that provides a more formal conceptualisation of a stimulus's temporal properties. For example, the CSC version of the *temporal difference* (TD) model treats the CS as a series of temporally ordered components that acquire associative strength (V) independently (Sutton & Barto 1987; cf. Moore et al, 1998). The final component, CS_n, conditions based on the error it has predicting the US, but the strength of that immediately preceding it, CS_{n-1}, changes according to the mismatch between its own V and the V of the final

component, and so on. V accruing to successive units is determined by a parameter gamma *(γ),* so that if CS_n acquires V of 1 unit, CS_{n-1} will acquire this strength discounted by γ - 0.9 units; CS_{n-2} will acquire CS_{n-1}'s strength discounted by γ - 0.81 units; etc. Learning during successive units is thus modulated by two parameters: a discount factor – gamma *(γ)* – that results in an exponential decay with time, and an *eligibility trace* which grows and declines for each CS component according to a constant, *delta.* Low delta values produce a rapid decay and curtailed conditioning; high values of gamma result in more conditioning to CS components earlier in the CS.

These assumptions feature in a recent computational model, SSCC TD (Mondragón, Gray, Alonso, Bonardi & Jennings, 2014), which incorporates the basic assumptions of TD and extends it to stimulus configurations. SSCC TD also computes total CS associative strength to mirror the single predictive value of the CS generated by trial-based theories, by averaging each individual component's associative strength over all the components, and estimates the total CR from this value (Gray, Alonso, Mondragón & Fernández, 2012). Importantly the model has successfully simulated Jennings et al.'s (2013) findings: a fixed CS gains more associative strength because each of its time-linked elements can reach asymptote. In contrast, although a variable CS comprises the same average number of time steps, many of its elements will be contiguous with the US on some trials, on which they gain V, but distant from the US on others, on which they overpredict US occurrence, and lose V. This ensures that elements comprising variable duration stimuli never reach a stable asymptotic value. Thus, unlike the elements comprising a fixed duration CS, the increase in associative strength of successive elements of a variable duration CS is not constant over time, but varies depending on the order and length of successive trials. SSCC TD could also simulate the results reported here. Thus this interpretation

of the present findings is much more easily accommodated by a trial-based approach.

A further problem for a time-accumulation model like RET is that it proposes that overshadowing is based on a decision process whereby responding is confined to the physically most salient cue (Gallistel & Gibbon, 2000). Thus RET could only explain these results by making the additional assumption that fixed duration CSs are more salient than variable CSs. Moreover, according to these accounts overshadowing is based on a decision rule; in any one animal it either occurs or not - it is not a graded effect, as trial-based models predict. In our experiments the overshadowing effect appeared to be graded; in this sense our findings are consistent with the trial-based view, and also with other reports in the literature (e.g. Kehoe, 1982; Thein, Westbrook & Harris, 2008; although see Balsam Drew & Gallistel, 2010). Nonetheless, although current formulations of time-accumulation models have difficulty with these results, it may be possible for their assumptions about the relative salience of fixed and variable cues to be further developed in order to accommodate these findings.

In summary, it seems that the associative, trial-based models might have the edge over the time accumulation accounts in explaining our findings. But such approaches have their limitations. As noted above, there is a lawful relationship between the ratio of the CS and ITI duration and both the speed with which the CR is acquired, and the rate of conditioned responding (e.g. Gibbon, Baldock, Locurto and Terrace, 1977; Holland, 2000; Lattal, 1999; Terrace, Gibbon, Farrell & Baldock, 1977), and it is a challenge for trial-based theories to explain such effects (although see e.g., Holland, 2000; Bouton & Sunsay, 2003). Moreover, timing accuracy is governed by Weber's law, such that the variability in timing is proportional to the duration of the interval being timed. This follows directly from the timing mechanisms incorporated into time-accumulation theories such as RET (Gallistel & Gibbon, 2000). It is not

yet clear how a trial-based account could begin to explain such regularities; thus, adapting themselves to accommodate such effects remains a significant challenge.

Finally, there is at least one alternative interpretation of our results which appeals to the notion of associability. Trial-based theories such as those proposed by Mackintosh (1975) and Pearce & Hall (1980) defined a property of a CS termed *associability* that can change with experience, and determine the ease with which the CS can become associated with a US (Mackintosh, 1975; Pearce & Hall, 1980). For example, latent inhibition training (Lubow & Moore, 1959), in which a CS is presented without consequence prior to conditioning, retards acquisition of the CR compared to the case in which no preexposure occurred, theoretically because the CS's associability falls during the preexposure phase. Such nonreinforced preexposure can also influence the ability of a CS to overshadow another: by slowing the speed with which the preexposed CS conditions, the degree to which the overshadowed cue can acquire associative strength is increased (e.g. Carr, 1974). It is thus possible that fixed and variable cues differ not in their ability to reach asymptote, but in their associability, and that this produced the effects we observed; although it is not immediately obvious how any current theories could explain how associability could be influenced by the temporal properties of the stimulus in this way, this must remain a logical possibility. Equally, it is possible that a specific conceptualisation of a CS's temporal properties could result in the prediction of greater overshadowing by a fixed CS, even without assuming that fixed and variable CSs acquire associative strength at different rates. But whether or not associability differences turn out to underlie our findings, our results imply that properties of a stimulus that vary trial-to-trial may have profound implications for learning - a conclusion that does not sit easily with time-accumulation models.

In conclusion, our results suggest that temporal information provided by the distribution form of the CS may play an important role in overshadowing, a result not easily explained by a range of time-accumulation models. In contrast, an adapted real-time trial-based model of conditioning was able to account for the pattern of results we present (Sutton and Barto, 1987; Mondragón et al., 2014). It appears that associative trial-based accounts of learning that are adapted to operate in real time might be best placed to offer a coherent account of the role of temporal CS factors on learning.

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Table 1

Group mean response rates during the preCS periods in the four training sessions of Experiment 1 (top panel) and Experiment 2 (lower panel).

Session	**1**	**2**	**3**	**4**
Lf	5.9	10.3	7.6	2.5
Lv	7.2	9.1	9.0	4.8
Nf/Lf	6.5	7.6	2.9	1.7
Nf/Lv	7.2	8.5	3.2	2.8
Nv/Lf	5.4	9.4	3.2	3.2
Nv/Lv	6.0	10.5	7.3	7.4

Session	**1**	**2**	**3**	**4**
Lf	6.8	8.2	4.0	2.0
Lv	4.7	8.3	4.0	4.0
Nf/Lf	3.3	3.2	0.8	1.0
Nf/Lv	4.3	2.9	0.8	1.2
Nv/Lf	5.4	3.9	1.4	1.3
Nv/Lv	5.0	5.6	4.7	2.6

Table 2

Experiment 2: Group mean corrected response rates during the noise in the four training sessions (top panel), and during the second noise test as a function of test trial distribution (lower panel).

Session	**1**	**2**	**3**	**4**
Nf/Lf	-1.1	9.9	6.8	12.8
Nf/Lv	-1.1	7.4	6.2	12.6
Nv/Lf	0.4	13.9	7.8	6.3
Nv/Lv	0.2	11.2	11.3	17.6

Test Trial Distribution	**Fixed**	**Variable**
Nf/Lf	26.0	14.9
Nf/Lv	19.7	11.9
Nv/Lf	25.3	14.1
Nv/Lv	33.5	14.0

Figure legend:

Figure 1. Schematic design of CS arrangement (Groups Lf, Nf/Lf, Nv/Lf, Lv, Nf/Lv and Nv/Lv).

Figure 2. Group mean corrected response rates during the light for Groups Lf, Lv, and during the noise/light compound for Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv (± 1 SE) in each of the four training sessions of Experiment 1.

Figure 3. Test sessions of Experiment 1**:** Top panel: Group mean corrected response rates during the light test trials. Bottom panel: Group mean overshadowing ratios for the overshadowing groups. C (control) Nf and Nv refer to whether the overshadowing stimulus was absent, fixed or variable, and Lf and Lv to whether the target CS was fixed or variable. Error bars show standard error of the mean.

Figure 4. Group mean responses per minute (± 1 SE) over the course of the fixed (Groups Nf/Lf and Nf/Lv) and variable (Groups Nv/Lf and Nv/Lv) duration noise during the compound trials of the final training session of Experiment 1. The data are presented in 3-s bins.

Figure 5. Group mean corrected response rates during the light for Groups Lf, Lv, and during the noise/light compound for Groups Nf/Lf, Nf/Lv, Nv/Lf and Nv/Lv (± 1 SE) in each of the four training sessions of Experiment 2.

Figure 6: Test sessions of Experiment 2**:** Top panel: Group mean corrected response rates during the light test trials. Bottom panel: Group mean overshadowing ratios for the overshadowing groups. C (control) Nf and Nv refer to whether the overshadowing stimulus was absent, fixed or variable, and Lf and Lv to whether the target CS was fixed or variable. Error bars show standard error of the mean.

Figure 7. Group mean responses per minute (± 1 SE) over the course of the fixed

(Groups Nf/Lf and Nf/Lv) and variable (Groups Nv/Lf and Nv/Lv) duration noise in Experiment 2. The data are presented in 3-s bins. Top panel: Data from the compound trials of the final training session. Bottom panel: Data from the probe trials of the final training session.

Figure 8: Scatter plot of individual overshadowing ratios for the light in each subject of Groups Nf/Lf and Nf/Lv, and Groups Nv/Lf and Nv/Lv in the two experiments.

Figure 1.

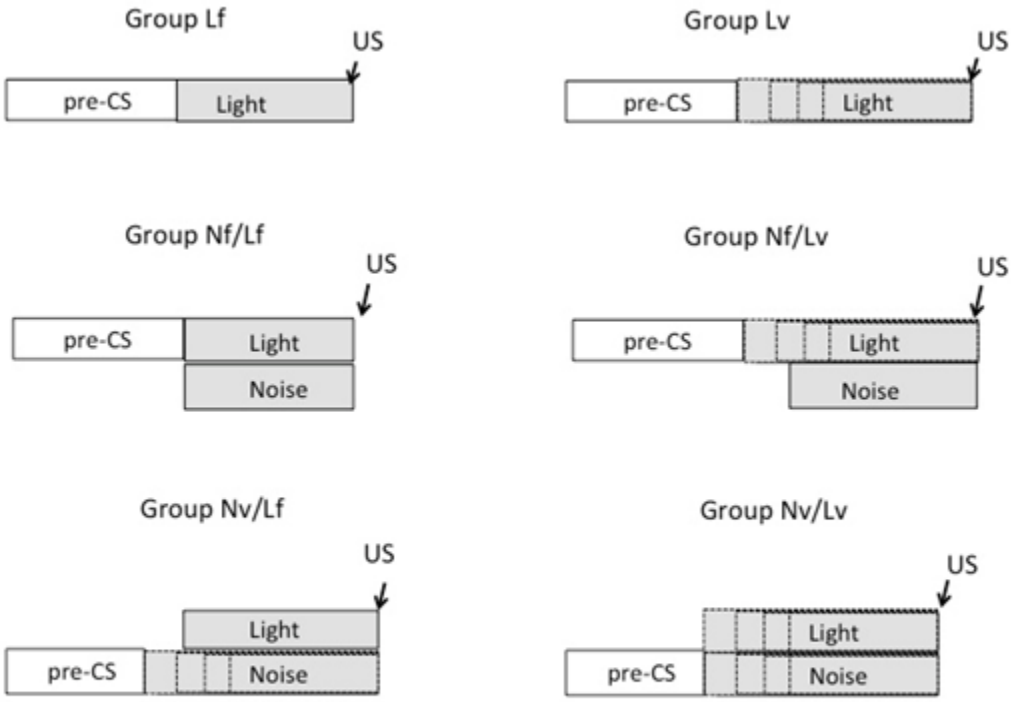

Group Lf
US
pre-CS
Light
Group Lv
US
pre-CS
Light
Group Nf/Lf
US
pre-CS
Light
Noise
Group Nf/Lv
US
pre-CS
Light
Noise
Group Nv/Lf
US
Light
pre-CS
Noise
Group Nv/Lv
US
Light
pre-CS
Noise

Figure 2.

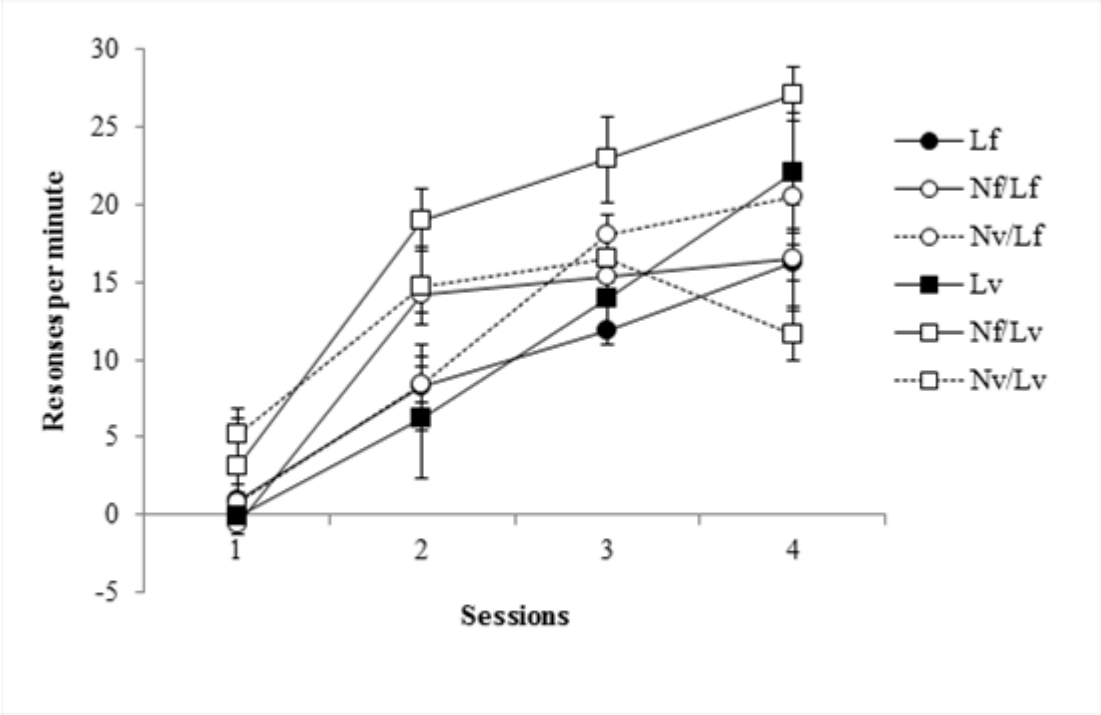
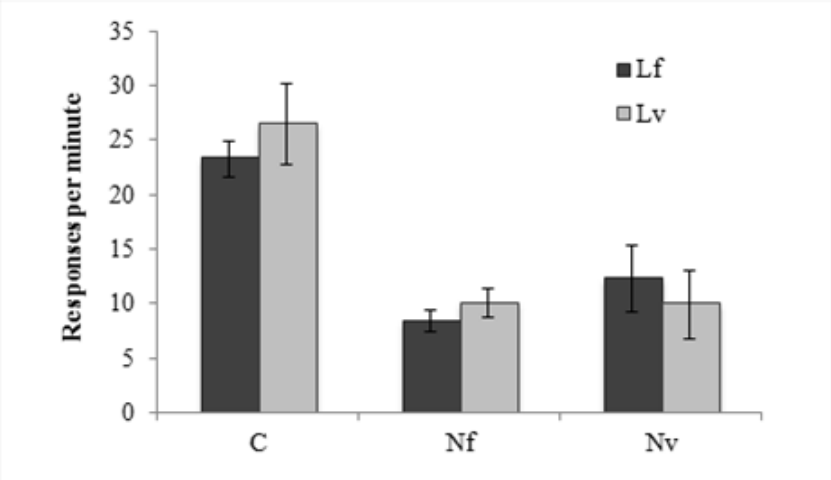

30
25
20
15
10
5
0
-5
Responses per minute
1
2
3
4
Sessions
Lf
Nf/Lf
Nv/Lf
Lv
Nf/Lv
Nv/Lv

Figure 3.


Responses per minute
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30
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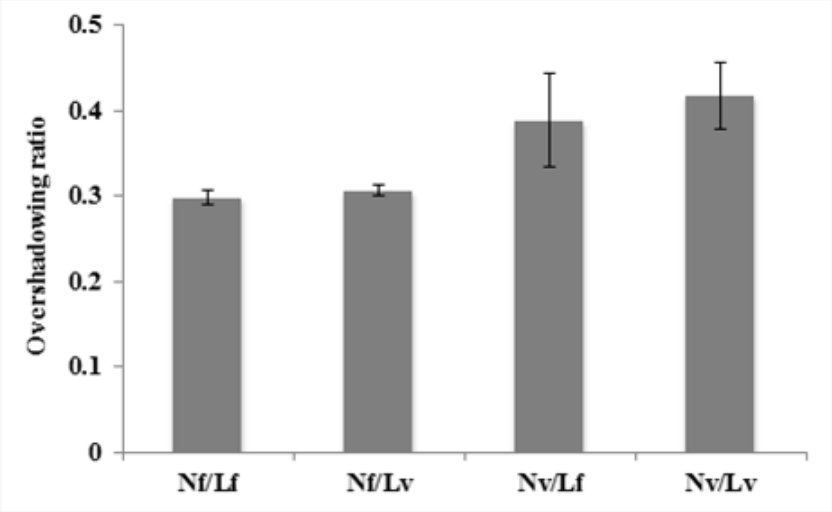
Lf
Lv
C
Nf
Nv


Overshadowing ratio
0.5
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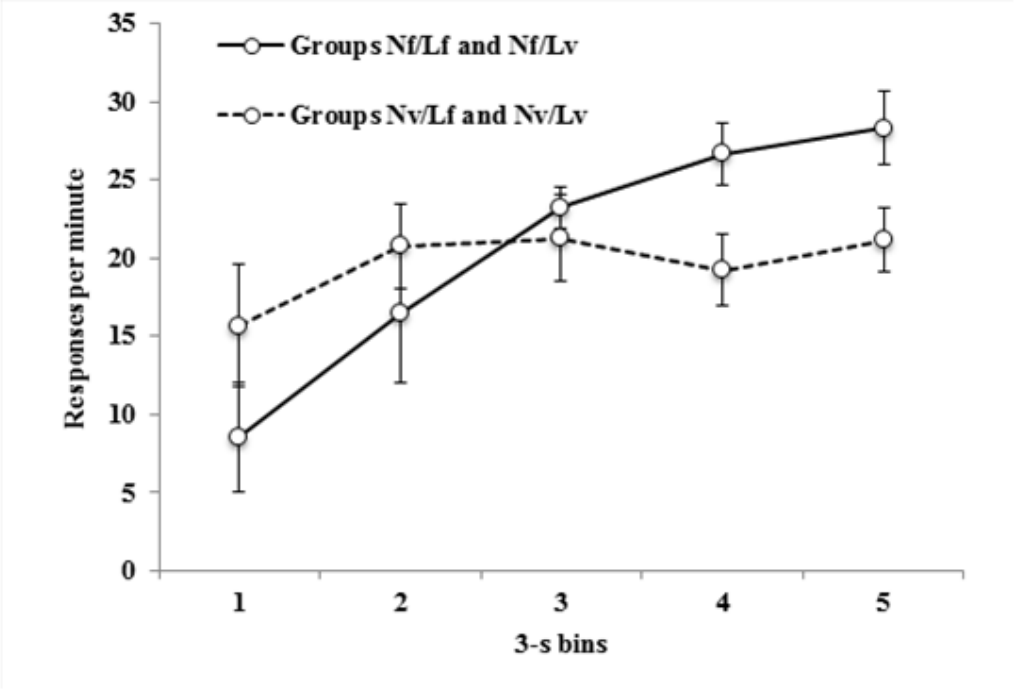
0.3
0.2
0.1
0
Nf/Lf
Nf/Lv
Nv/Lf
Nv/Lv

Figure 4.


Groups Nf/Lf and Nf/Lv
Groups Nv/Lf and Nv/Lv
Responses per minute
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30
25
20
15
10
5
0
1
2
3
4
5
3-s bins

Figure 5.

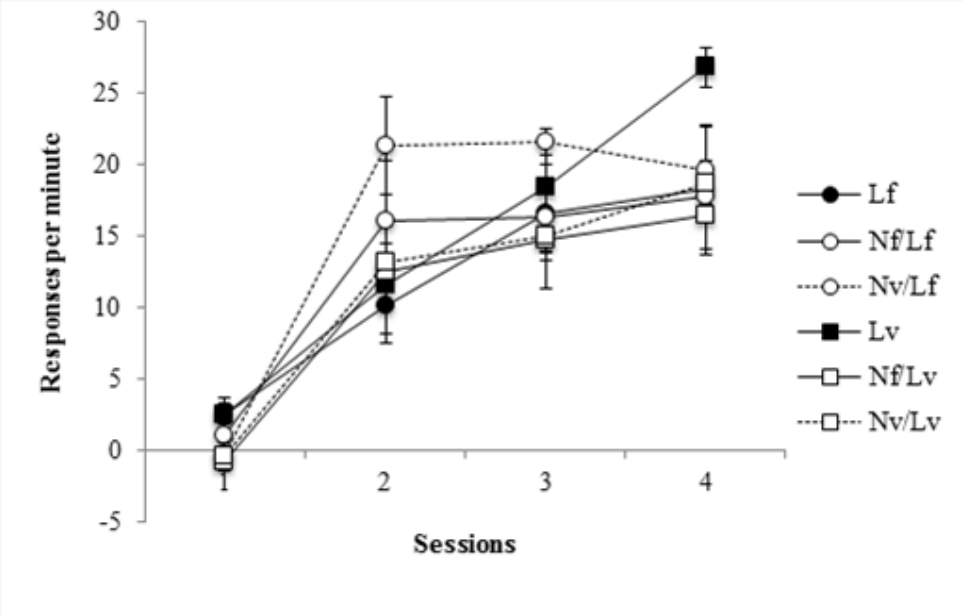
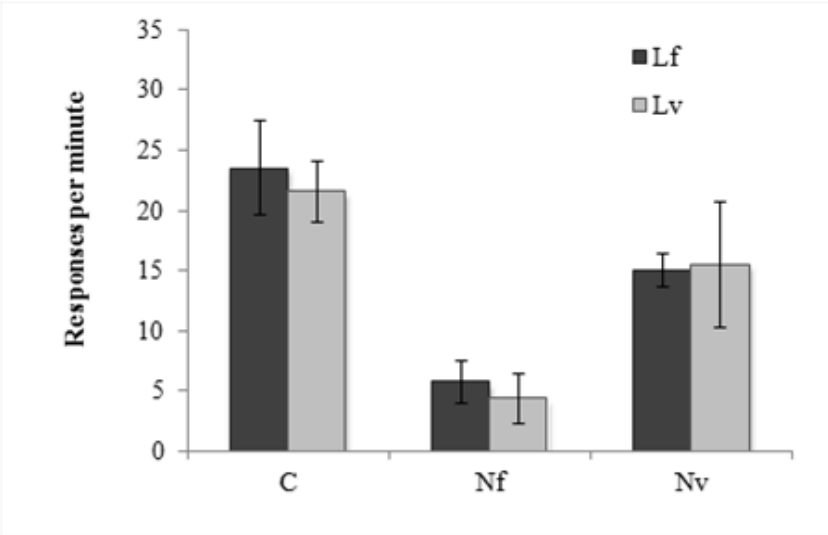

30
25
20
15
10
5
0
-5
Responses per minute
1
2
3
4
Sessions
Lf
Nf/Lf
Nv/Lf
Lv
Nf/Lv
Nv/Lv

Figure 6.


Responses per minute
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30
25
20
15
10
5
0
Lf
Lv
C
Nf
Nv

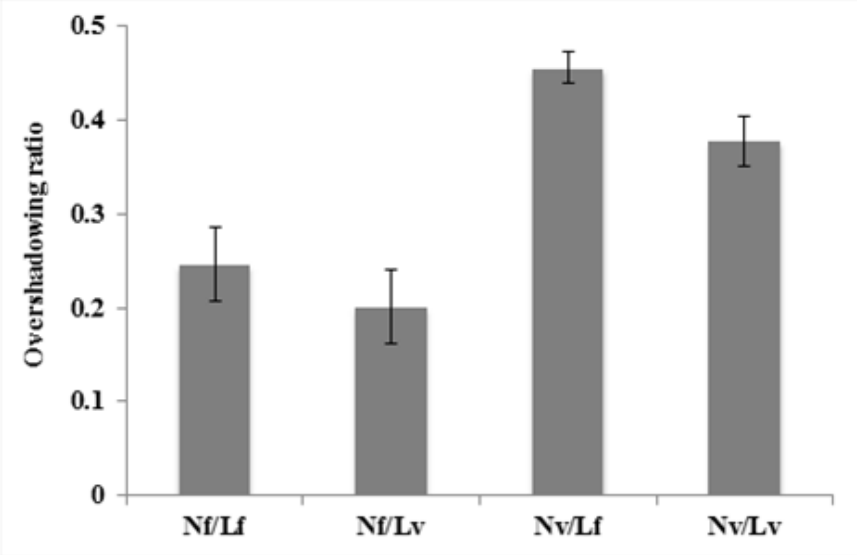

Overshadowing ratio
0.5
0.4
0.3
0.2
0.1
0
Nf/Lf
Nf/Lv
Nv/Lf
Nv/Lv

Figure 7.

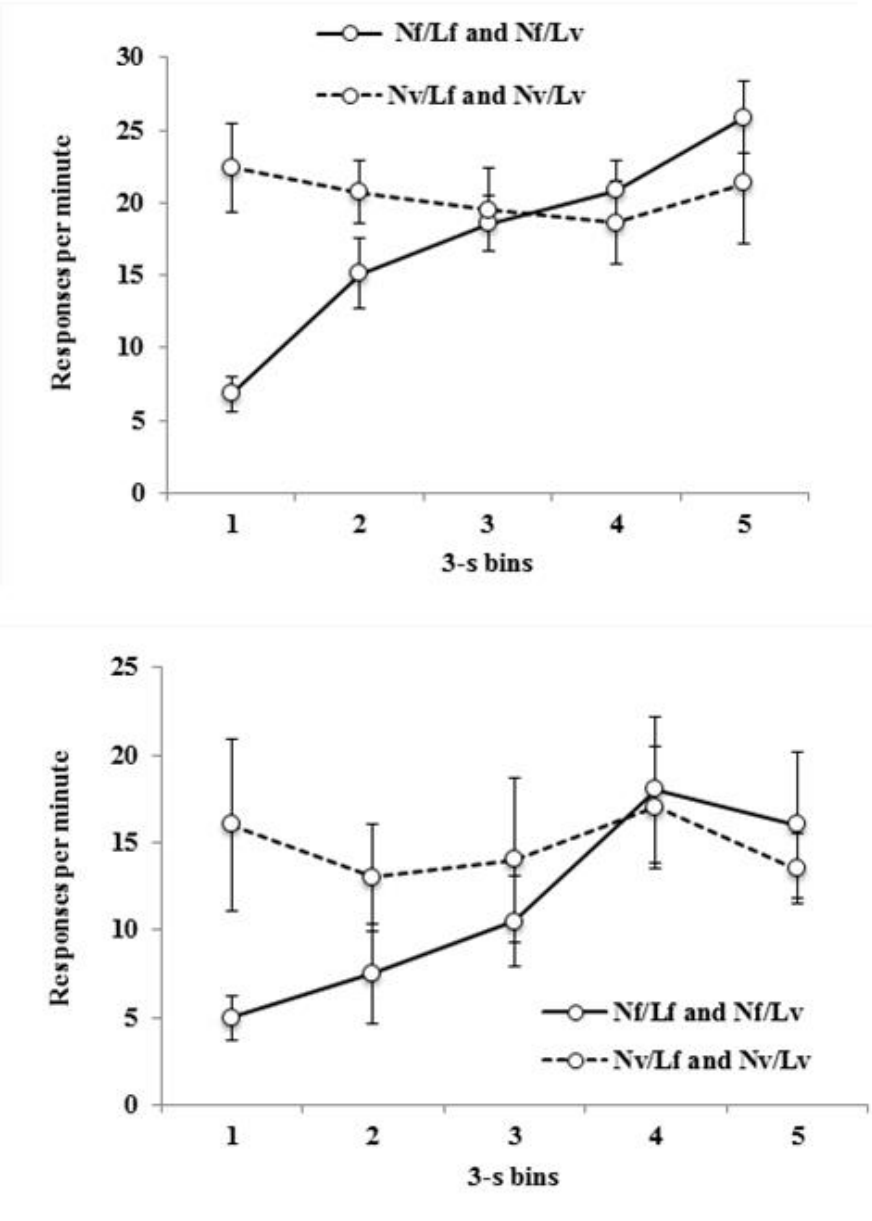
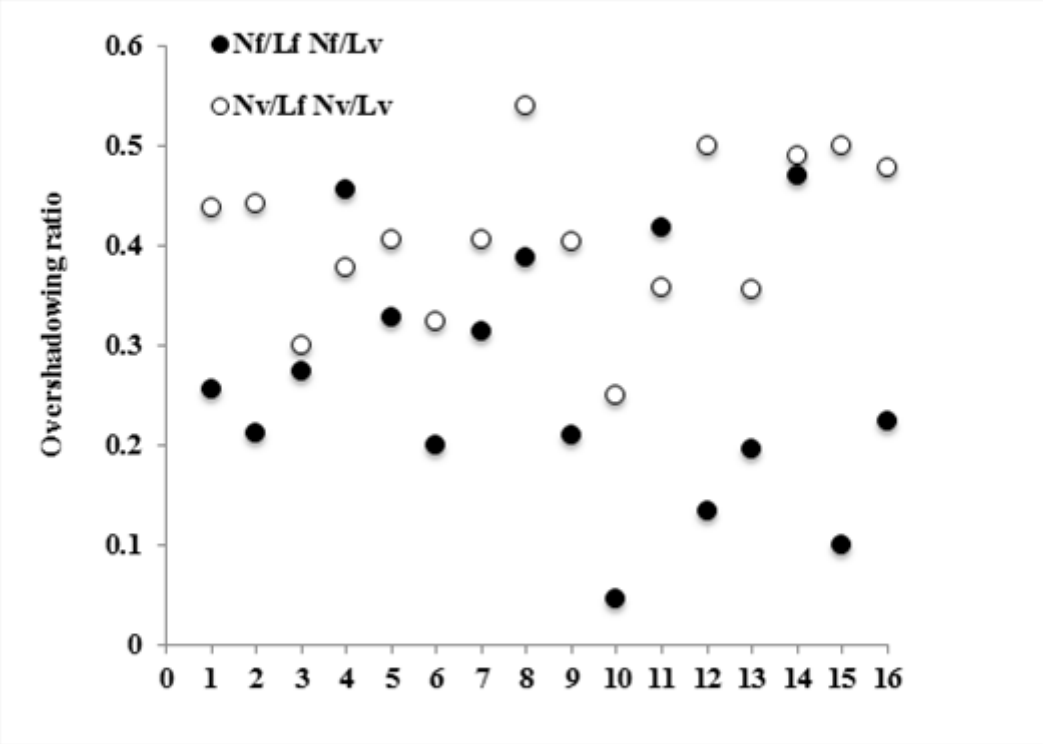

Nf/Lf and Nf/Lv
Nv/Lf and Nv/Lv
Responses per minute
30
25
20
15
10
5
0
1
2
3
4
5
3-s bins
Responses per minute
25
20
15
10
5
0
Nf/Lf and Nf/Lv
Nv/Lf and Nv/Lv
1
2
3
4
5
3-s bins

Figure 8.


Nf/Lf Nf/Lv
Nv/Lf Nv/Lv
Overshadowing ratio
0.6
0.5
0.4
0.3
0.2
0.1
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16