

Blocking by fixed and variable stimuli: Effects of stimulus distribution on blocking.

Dómhnall J. Jennings¹ & Charlotte Bonardi²

¹ Institute of Neuroscience, Newcastle University, Newcastle upon Tyne NE2 4HH, UK.

² School of Psychology, University of Nottingham, Nottingham NG2 2RD, UK.

Corresponding author: Charlotte Bonardi (cmb@psychology.nottingham.ac.uk)

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Running Head: Stimulus distribution effects on blocking.

Abstract

An experiment with rats compared the ability of fixed and variable duration cues to produce blocking. Rats in Group B (Blocking) were trained that both fixed- (*F*) and variable- (*V*) duration cues would be followed by food delivery. In a subsequent training stage *F* and *V* continued to be reinforced, but *F* was accompanied by *X*, and *V* by *Y*. In the test phase responding to *X* and *Y* was examined. Control Group O (Overshadowing) received identical treatment, except that *F* and *V* were nonreinforced in the first training stage. In Group B there was evidence for blocking, but only of *X* which had been conditioned in compound with the fixed-duration *F*; there was no evidence for blocking of *Y*, which had been conditioned in compound with the variable duration *V*. It is suggested that this result may occur because fixed cues reach a higher, more stable asymptote of associative strength than their variable equivalents.

Keywords:

Associative learning, stimulus distribution form, blocking, timing, rats

Introduction

In a typical classical conditioning task a neutral, *conditioned stimulus* (CS) of a fixed duration is followed by delivery of a motivationally significant outcome, the *unconditioned stimulus* (US). Thus the CS comes to act both as a signal both *that* and *when* the US will occur (conditioning and timing respectively). Despite the intimate relation between these two types of learning, theories of conditioning and timing have developed relatively independently, and only recently has the relationship between temporal features of the CS and conditioning been explored. For example, in a series of experiments in rats, Jennings et al. (2013) compared levels of conditioned responding to fixed-duration CSs with responding to CSs whose duration varied from trial to trial. Even under equivalent testing conditions, fixed-duration cues elicited higher levels of responding than variable-duration cues of the same mean duration. In a later study Bonardi et al. (2014) found that overshadowing was more profound when the overshadowing cue was fixed duration than when it was variable.

They interpreted these findings in terms of a real-time model of conditioning, temporal difference (TD) learning (Sutton & Barto, 1987; 1990). They differ from other associative models by conceptualising the CS as a series of temporally ordered elements that independently acquire associative strength (e.g. Sutton & Barto, 1990; Vogel Brandon & Wagner, 2003). A recent version of this model has been developed which allows it to compute learning for both serial and simultaneous stimulus compounds (Mondragón, et al., 2012). This *SSCC TD* model was able to simulate our (2013) findings, predicting that fixed-duration stimuli acquire a higher, more stable asymptote of associative strength than their variable counterparts (Jennings et al., 2013; Mondragón, et al., 2012). This is because each of the time-linked elements of a fixed CS can reach asymptote; in contrast, even though a variable CS comprises the same average number of temporal elements as the fixed, many of

these will be contiguous with the US on some trials and gain associative strength, but distant from the US on other trials and therefore lose it. This constant fluctuation ensures that variable stimuli elements never reach a stable asymptote. As associative strength is assumed to be monotonically related to performance on a conditioning task, this would explain why fixed-duration CSs elicited more conditioned responding. It could also make such cues better competitors for associative strength when they are conditioned in compound with another stimulus. For example, according to two influential accounts of conditioning, (Pearce & Hall, 1980; Rescorla & Wagner, 1972) a given US can support only a limited amount of associative strength. Thus when conditioning compound AX, the more strength that is acquired by A, the less is available for X (see also Mackintosh, 1975; Wagner, 1981).

This study tested another implication of this account -- that fixed duration CSs produce better blocking than variable CSs. Two groups of rats were trained with fixed and variable duration cues, *F* and *V*; for Group B (blocking) *F* and *V* were reinforced whereas for Group O (overshadowing) they were not (see Table 1). To equate the groups' experience they were also trained with a second pair of cues, *Fc* and *Vc*. Again, *Fc* was fixed and *Vc* variable, and were both reinforced in Group O but nonreinforced in Group B (cf., Rescorla, 1999). Then all rats experienced two reinforced stimulus compounds, of *F* with *X*, and of *V* with *Y*, and finally performance to *X* and *Y* was examined. In stage 2 *F* and *V* had the opportunity to block acquisition of associative strength by *X* and *Y*. If fixed CSs reach a higher, more stable asymptote than variable cues they should produce better blocking, and *X* should support less conditioned responding than *Y* at test.

A second aim was to evaluate an alternative interpretation of Bonardi et al.'s (2014) results. Many trial-based theories of conditioning assume that any stimulus has a level of *associability* which determines the speed with which it conditions (e.g. Pearce & Hall, 1980). If fixed duration cues have *higher associability* than variable CSs, it could explain their

greater ability to compete for associative strength, and produce overshadowing. However, associability differences would be less likely to affect blocking, because here (unlike overshadowing) *F* and *V* must be conditioned before their ability to compete for associative strength is assessed. It is usually assumed that associability declines over the course of conditioning, as the outcome is fully predicted (Mackintosh, 1975; Pearce & Hall, 1980); thus any difference in associability between fixed and variable cues will have diminished before their ability to produce blocking is evaluated. Thus if fixed duration cues still produce more effective blocking, this would be more difficult to interpret in terms of associability differences. To strengthen this logic, stage 1 training was continued until levels of responding to *F* and *V* in Group B had asymptoted. If conditioned responding is an index of associative strength, this is consistent with the associative strength of the fixed and variable cues having reached asymptote, further minimising differences in their associability before the start of compound training. Thus if Bonardi et al.'s results (2014) arose because fixed cues have higher associability, they would not necessarily produce better blocking in this study.

Method

Subjects:

Subjects were 32 male Lister hooded rats (Charles River UK) with a mean free-feeding weight of 308 g (range: 275-330 g). They were weighed daily and their daily food ration restricted so they gradually reduced to 85% of their free-feeding weights before the start of training. They were maintained at this level, their target 85% level being adjusted weekly according to a growth curve so that their target weights increased gradually over the course of the experiment. Water was freely available in the home cages. The holding room was on a 12-hour light/dark cycle, with lights being turned on at 7am, and temperature was maintained at 21°C (± 1); the humidity was 60% (± 10). There were 16 animals per group.

Apparatus:

All testing was conducted in eight identical chambers (20 x 24 x 30 cm), each situated in a ventilated, noise-attenuating shell (74 x 38 x 60 cm; MED Associates). Each chamber was equipped with a foodcup, into which 45-mg Noyes (Improved Formula A) food pellets could be delivered by a pellet dispenser (Model ENV-203). Each head entry into the food cup was recorded, by the breaking of an infra-red photobeam, as a response. Each chamber had a 2.8-W houselight 11 cm above the food cup, the bottom half of which was shielded, that was illuminated throughout the experimental session, and a speaker, on the right side of the back wall of the chamber opposite the food cup, which could deliver a white noise, a 10-Hz click, a 2-kHz tone and a 4-kHz tone, all approximately 75dB (scale A, measured near food cup). There were two 2.8-W jewel lights, one 2.5cm to each side of the food cup; the left light was kept on throughout its scheduled presentations, and the right light was always pulsed (.33s on and .33s off). Med-PC for Windows (Tatham & Zurn, 1989) controlled experimental events.

Procedure

Stage 1: Each of the 12 sessions in this stage comprised 10 presentations each of F , V , Fc and Vc intermixed in a semi-random order (see Table 1). F and Fc were of a fixed 10-s duration, but the durations of V and Vc varied from trial to trial with a mean of 10s (all variable durations were drawn from an exponential distribution). The mean duration of V and Vc over all sessions of this stage was 9.34s and 10.46s respectively for Group B, and 9.77 and 10.98s for Group O. For Group B F and V were each followed by delivery of a food pellet, while Fc and Vc were not; the reverse was true for Group O. For half of each group F was click and V noise, and Fc high tone and Vc low tone; for the remainder F was noise and V click, and Fc low tone and Vc high tone. The intertrial interval (ITI) comprised a fixed 80-s

interval plus a variable component with a mean of 60s. The 20-s portion of the ITI that immediately preceded each stimulus presentation served as the pre-CS period.

Stage 2: Each of the 4 sessions in this stage comprised trials on which *F* was accompanied by *X*, and *V* by *Y*. *X* and *Y* were visual, illumination of one of the two lights. For half the rats in each group, *X* and *Y* were a fixed 10-s, and for the rest they were variable with a mean of 10s. These 4 subgroups were counterbalanced for stimulus identity: for half the rats in each subgroup *F* was click and *V* noise, and *Fc* high tone and *Vc* low tone etc (see above). The click was always presented with the left light, and the noise with the right light; thus *X* and *Y* were fully counterbalanced for stimulus identity. When both stimuli were fixed, or both variable, they started and ended simultaneously; when one was fixed and the other variable, they terminated together. All stimulus presentations were followed by the delivery of a food pellet. These sessions were otherwise identical to those of Stage 1.

Test: The three test sessions were identical to those of Stage 2 except that 20 trials, 10 with *FX* and 10 with *VY*, were replaced by test trials with *X* or *Y* alone, 10 of each. All test trials were a fixed 10s in duration, and 4 *X* and 4 *Y* trials were followed by the delivery of a food pellet; the remaining 6 *X* and 6 *Y* trials were nonreinforced.

Data Treatment

The mean response rates during each trial type were obtained by computing the total number of responses made during each CS type in each session, and during the corresponding preCS periods, and converting to responses per minute (rpm). Conditioned responding was indexed by a *difference* score - mean response rate during each CS type after subtraction of the rate during the preCS period.

Number of responses in successive 1-s time bins of the reinforced CSs in stage 1 was used to calculate the response rate in each bin for each rat, pooled over 2 6-session bins. For the variable CS computation of response rate took into account the number of trials on which the CS was present in each bin. The response rate functions were normalized, and a linear function fitted to each normalised response rate function, and the slope determined from the best-fitting linear curve for each rat (Bonardi et al., 2014). The temporal slopes were compared against a mean of zero using one-sample t-tests, using the Bonferroni correction.

Data were subject to mixed ANOVA; significant two-way interactions were explored with simple main effects using the pooled error term. Partial η^2 is given as a measure of effect size for significant main effects and interactions.

Results

Stage 1: Difference scores for Stage 1 are shown in Figure 1. Responding increased to the reinforced cues (F and V in Group B, Fc and Vc in Group O) but remained low to the nonreinforced cues (Fc and Vc in Group B, F and V in Group O). Responding seemed higher in Group B than in Group O during later sessions, and higher to the fixed F and Fc than to the variable V and Vc on reinforced trials. To assess if asymptote had been reached, data were analysed in three, four-session blocks, with session as a factor within each block. ANOVA with group (B/O), reinforcement, fixed/variable (F/Fc versus V/Vc), block (1-3) and session (1-4) as factors revealed significant effects of block, $F(2, 60) = 69.45, p < .001, MSe = 210.81, \eta_p^2 = .70$, session, $F(3, 90) = 86.66, p < .001, MSe = 29.89, \eta_p^2 = .74$, fixed/variable, $F(1, 30) = 11.58, p = .002, MSe = 54.33, \eta_p^2 = .28, CI = [.05, .49]$, and reinforcement, $F(1, 30) = 305.22, p < .001, MSe = 599.46, \eta_p^2 = .91$, two-way interactions of block and session, $F(6, 180) = 25.78, p < .001, MSe = 59.72, \eta_p^2 = .46$, block and reinforcement, $F(2, 60) = 111.91, p < .001, MSe = 199.10, \eta_p^2 = .79$, session and reinforcement, $F(3, 90) = 46.87, p < .001, MSe = 199.10, \eta_p^2 = .79$.

.001, $MSe = 31.83$, $\eta_p^2 = .61$, and a three-way interaction between these three factors, $F(6, 180) = 7.78$, $p < .001$, $MSe = 57.77$, $\eta_p^2 = .21$; the fixed/variable x reinforcement interaction was also significant, $F(1, 30) = 7.79$, $p = .009$, $MSe = 71.63$, $\eta_p^2 = .21$. Nothing else was significant, largest $F(1, 30) = 3.02$, $p = .09$, $MSe = 599.46$.

The three-way interaction between block, session and reinforcement was explored with 2-way ANOVAs, with block and session as factors, on the data from reinforced and nonreinforced trials. For reinforced trials this yielded a significant interaction, $F(6, 186) = 15.70$, $p < .001$, $MSe = 108.2$, $\eta_p^2 = .34$, and an effect of session on block 1, $F(3, 93) = 128.69$, $p < .001$, $MSe = 53.03$, and block 2, $F(3, 93) = 8.37$, $p < .001$, $MSe = 53.03$, but not block 3, $F(3, 93) = 1.85$, $p = .14$, $MSe = 53.03$. A parallel ANOVA on nonreinforced trials also revealed a significant interaction, $F(6, 186) = 23.77$, $p < .001$, $MSe = 12.22$, $\eta_p^2 = .43$, and an effect of session on block 1, $F(3, 93) = 74.9$, $p < .001$, $MSe = 8.32$, and block 2, $F(3, 93) = 8.22$, $p < .001$, $MSe = 53.03$, but not block 3, $F < 1$. Thus responding to both reinforced and nonreinforced CSs was steady over the last block of training, suggesting that conditioning responding had reached asymptote.

Exploration of the Fixed/variable x Reinforcement interaction confirmed that on reinforced trials response rates were higher during the fixed stimuli, $F(1, 60) = 18.83$, $p = .001$, $MSe = 62.98$. This was not the case on the nonreinforced trials, $F < 1$. This is consistent with the hypothesis that fixed CSs gain more associative strength than variable CSs.

To lend further weight to the implication of the previous analysis that conditioned responding had reached asymptote, we conducted a Bayesian analogue of the paired t-test (Rouder et al., 2009; <http://pcl.missouri.edu/bayesfactor>). This allows quantification of evidence for the null hypothesis (Wagenmakers, 2007); it assumes effect sizes that equal zero under the null hypothesis, but differ from zero under the alternative hypothesis, and yields a Bayes factor indicating how much more likely the null hypothesis is than the alternative. We

employed the F values relating to the change in responding on reinforced, and nonreinforced, trials between the first and last two sessions of the final test block. This yielded scaled Bayes factors of 4.03 and 5.27 for reinforced and nonreinforced trials respectively; as values of ≥ 3 may be taken as evidence for the null hypothesis (Jeffreys, 1961), we take this as further evidence that conditioning had reached asymptotic levels on both types of trial.

Group mean rates of preCS responding (over all trial types) in each session were 3.58, 4.73, 3.54, 2.07, 1.20, 1.11, 0.96, 0.70, 0.97, 1.20, 0.94 and 0.86 rpm for Group B, and 4.79, 6.52, 4.10, 2.73, 1.78, 1.53, 1.40, 1.29, 1.28, 1.17, 1.13 and 1.10 rpm for Group O. ANOVA with group and sessions as factors revealed an effect of group, $F(1,30) = 4.22, p = .049, MSe = 8.35, \eta_p^2 = .03, CI = [.00, .34]$ reflecting a slightly higher rate of responding in Group B; the magnitude of this difference, at less than 2 rpm, was very small and unlikely to have much impact on the difference scores. There was also an effect of block, $F(2, 60) = 93.76, p < .001, MSe = 14.75, \eta_p^2 = .76, CI = [.64, .82]$, sessions, $F(3, 90) = 13.45, p < .001, MSe = 7.78, \eta_p^2 = .31, CI = [.14, .43]$, and a Block x Sessions interaction, $F(6, 180) = 9.72, p < .001, MSe = 6.49, \eta_p^2 = .24, CI = [.12, .32]$; there was an effect of sessions on block 1, $F(3, 270) = 32.38, p < .001, MSe = 6.92$, but not blocks 2 and 3, $F_s < 1$.

We also anticipated that the distribution of responding should differ across the fixed and variable CSs, increasing over the course of the fixed CS, but remaining steady over the variable CS. This would result in higher slopes in the fixed CS - but we did not find strong evidence for this. These data were computed for the first and second half of the training stage, to reduce noise (timing data are routinely collected over a relatively large number of trials). Mean slopes for fixed and variable cues in Group B were 0.24 and 0.28 in the first half, and 0.95 and 1.01 in the second half; corresponding values for Group O were 0.57 and 0.18, and 0.43 and 0.51. ANOVA with Group (B/O), fixed/variable and block as factors revealed only a main effect of half, $F(1, 30) = 6.90, p = .013, MSe = 0.77, \eta_p^2 = .19, CI =$

[.01, .41]; nothing else was significant, largest $F(1, 30) = 4.14, p = .051, MSe = 0.77$; but a one-sample t-test conducted on the slopes for fixed and variable stimuli in each half revealed that on all slopes were greater than zero, $ps < .02$, except for the slope for the variable cues in the first half of training 1, $p = .17$ (uncorrected). This is consistent with the suggestion that, at least early in training, the slopes for the fixed cues were higher than for the variable cues.

Stage 2: In this phase one rat in Group O responded at a much lower rate (> 2.5 standard deviations from the mean) than any other rat, which casts doubt over whether it learned anything during the compound phase. Thus this animal's data were omitted from all subsequent analyses. The Stage 2 data appear in Figure 1 (top panel, right). In Group B responding to F and V was maintained after addition of X and Y , while in Group O responding to F and V , which had been nonreinforced during Stage 1, rapidly increased.

ANOVA with group (B/O), fixed/variable (F/V) and session as factors revealed a main effect of sessions, $F(3, 87) = 24.27, p < .001, MSe = 98.63, \eta_p^2 = .46$, which interacted with group, $F(3, 87) = 4.00, p = .01, MSe = 98.63, \eta_p^2 = .12$; nothing else was significant, largest $F(1, 29) = 2.57, p = .12, MSe = 144.41$. Responding was higher in Group B on session 13, $F(1, 116) = 4.27, p = .041, MSe = 312.11$, but not on any other session, $F_s < 1$.

Mean rates of preCS responding in each session were 1.56, 1.46, 1.37 and 1.50 rpm for Group B, and 4.60, 2.77, 2.49 and 2.73 rpm for Group O - marginally higher in Group O. ANOVA with group and sessions as factors revealed main effects of group $F(1, 29) = 21.64, p < .001, MSe = 4.01, \eta_p^2 = .43$ and session $F(3, 87) = 6.25, p = .001, MSe = 1.34, \eta_p^2 = .18$, and an interaction between these factors, $F(3, 87) = 4.84, p = .004, MSe = 1.34, \eta_p^2 = .14$; preCS responding was lower in Group B on all four sessions, smallest $F(1, 116) = 4.79, p = .031, MSe = 2.01$. This could be due to the pretrained F and V blocking the context in Group B. In Group O the previously nonreinforced F and V were now for the first time followed by

food, but in Group B unexpected delivery of food after X and Y would be blocked by F and V , which could also reduce any context conditioning occurring on these trials, thus reducing preCS responding in these animals.

Test: Responding to X and Y is shown in Figure 1 (lower panel). Responding to X in Group B appeared lower than in the other conditions, which seemed not to differ. ANOVA with group (B/O), fixed/variable (X/Y) and session as factors revealed an effect of fixed/variable, $F(1, 29) = 5.86, p = .022, MSe = 40.15, \eta_p^2 = .17$ which interacted with group, $F(1, 29) = 5.41, p = .027, MSe = 40.15, \eta_p^2 = .16$. The effect of fixed/variable was significant in Group B, $F(1, 29) = 11.64, p = .002, MSe = 40.15$, but not in Group O, $F < 1$, and responding was lower in Group B than in Group O during X , $F(1, 58) = 5.18, p = .027, MSe = 131.57$, but not during Y , $F < 1$. Nothing else was significant, largest $F(2, 58) = 2.14, p = .13, MSe = 44.51$ for the effect of session. Group mean rates of preCS responding in the three sessions were 1.88, 1.47 and 1.75 rpm for Group B, and 1.74, 1.71 and 1.97 rpm for Group O. ANOVA with group and sessions revealed nothing significant, $F_s < 1$. This confirms that the rates of baseline responding from which the difference scores were derived did not differ systematically among the various conditions.

General Discussion

In the present experiment only the fixed duration cue F produced a reliable blocking effect. We did not, however, find that F also produced better overshadowing in Group O -- responding to X and Y did not differ in Group O (although it should be acknowledged that we did not include an overshadowing control group in this experiment). This would contrast with our previous findings (Bonardi et al. 2014); however the experiments differed in a number of

ways. In particular, in this study rats had extensive experience of the blocking/overshadowing cues *F* and *V* before the compound phase, which would be expected to reduce their associability (Mackintosh, 1975; Pearce & Hall, 1980) and thus reduce the degree to which they could produce overshadowing. In contrast, in the experiment reported by Bonardi et al. (2014) the overshadowing cues were completely novel at the start of compound training. The stage 1 preexposure of *X* and *Y* in Group O could have other effects; for example, such differential training might perhaps result in *F* and *V* becoming net conditioned inhibitors, and thus being able to produce superconditioning of *X* and *Y* in stage 2 - thus exaggerating the size of the observed blocking effect. However, inhibitory conditioning after differential conditioning is not anticipated by standard associative models; for example, Rescorla & Wagner (1972) would predict that any inhibitory learning to *F* and *V* would stem from the nonreinforcement of these stimuli in an excitatory context, which would result in a neutral compound of *F* (or *V*) and the context. Thus *F* and *V* could only produce superconditioning in stage 2 if it were conducted in a different and less excitatory context. Moreover, theory aside, there is little evidence in the literature for such a differential inhibition effect; although Williams, Travis & Overmier (1986) found evidence for inhibition after such differential conditioning, this was in a shock conditioning procedure in which the initial conditioning stage was conducted off baseline. This could produce precisely the type of context change that we have argued would be required to reveal such a differential inhibition effect.

Finding that a fixed duration CS produces better blocking than a variable CS is consistent with our proposal that fixed duration cues reach a higher, more stable asymptotic level of associative strength. This conclusion does, of course, rely on the assumption that ability to produce blocking is a measure of associative strength - and there are alternative interpretations (cf. Ward et al., 2012; see further discussion below). Our results are less consistent with the alternative hypothesis, that fixed duration stimuli produce more

overshadowing or blocking because they have higher associability. As both fixed and variable cues receive conditioning before their ability to produce blocking is assessed, levels of associability should be relatively low, and thus any associability differences relatively small (Mackintosh, 1975; Pearce & Hall, 1980). We attempted to reduce such potential associability differences even further by conditioning both X and Y to asymptote before the start of the compound phase. However, although conditioned responding is thought to be monotonically related to associative strength, it is still possible that associative strength was increasing even though conditioned responding had asymptoted. Thus we have no direct evidence that asymptotic levels of associative strength had been reached (and it is difficult to see how such evidence could be obtained. Nonetheless, we would argue that these considerations make an explanation of our results in terms of associability less plausible.

These findings add to a growing body of literature illustrating the effects of temporal variables on associative learning. But although many theories from both conditioning and timing traditions have been proposed to explain such learning, most of them cannot explain our results. Kirkpatrick (2014) classified these models into three broad classes:

Time-based hybrid models: Some accounts of this type allow time of reinforcement to be accurately encoded by assuming that the CS is represented in a form that varies as a function of time. This may be because CS onset initiates activity in a series of oscillators with different periods (Church & Broadbent, 1990), or activates a series of memory traces (Machado, 1997), or provokes some other time-based process that uniquely defines different portions of the CS (cf., Grossberg & Schmajuk, 1989). Another set of models in this class supposes timing arises through some computation based on processing of a previously experienced reinforcer (e.g. Kirkpatrick, 2002; Staddon & Higa, 1996). However, the majority of these models cannot explain cue competition effects such as blocking, and those

that can do not allow it to be influenced by temporal variables (Kirkpatrick, 2014).

Information processing models: These models assume sensitivity to temporal information in the conditioning episode, allowing computation of the rate of reinforcement during environmental events. If reinforcement rate during the CS exceeds that in the background, the CR is produced (Gibbon & Balsam, 1981; cf. Rate Expectancy Theory RET Gallistel & Gibbon, 2000). Some of these accounts can also explain cue competition within this alternative theoretical framework; for example, RET assumes that when the novel cue is added during a blocking task the rate of reinforcement is attributed solely to the blocking cue (cf., Balsam & Gallistel, 2009; Kirkpatrick & Church, 2003), producing a blocking effect. Most of these accounts assume that temporal information is summed across trials, such that fixed and variable duration cues would be treated as equivalent if their overall duration is matched, meaning they could not explain the present findings. However, in one variant of RET, Balsam and Gallistel (2009) suggested that the CS's information value influences conditioned responding: as fixed CSs are more informative than variable CSs, they should condition more quickly (Balsam & Gallistel 2009; Ward et al., 2012). In fact attempts to verify this prediction have not supported this model: Ward et al. (2012) found no difference in the speed of acquisition by fixed and variable CSs, whereas Jennings et al. (2013) reported that variable cues developed conditioned responding faster than fixed CSs - the *opposite* to what this account predicts. But as a difference in a CS's information value might also influence its ability to produce blocking, our results might provide an alternative means of evaluating this theory. For example, if the blocking cue were fixed, addition of a target cue would add little further information, regardless of whether it was fixed or variable. But if the blocking/overshadowing cue were variable, addition of a fixed target *could* add further information, and so therefore elicit higher levels of conditioned responding than a variable

target cue. This does stretch the model to an extent - if blocking is based on a decision to attribute the CR to the CS that provides the most information, then the pre-conditioned blocking stimulus will always be more informative than the unconditioned target stimulus, and variations in the degree to which this is the case should not affect the outcome of the decision process. Nonetheless, to investigate this possibility we reanalysed our test data, with whether the target cue was fixed or variable as a factor. This yielded a significant interaction between whether the blocking/overshadowing cues and the target cues were fixed or variable; but this reflected lower responding to the fixed than to the variable target when the blocking/overshadowing cue was fixed, *not* when it was variable -- the opposite to what this theory predicts¹.

Prediction error-based hybrid models: Although most conditioning models do not consider the temporal structure of the CS, there are exceptions. The temporal coding hypothesis (Matzel, Held & Miller, 1988) assumes that associations incorporate temporal information about the CS-US pairing (e.g. Barnet, Grahame & Miller 1993). But this model predicts that blocking will be maximal if the temporal information in the blocking cue matches that of the blocked cue. In our study this predicts that *F* will produce more blocking than *V* when *X* was fixed, but *less* when *X* was variable. As in our study half the animals had a fixed-duration *X* and *Y*, and the other half a variable-duration *X* and *Y*, this would predict no overall difference in blocking - which was not what we observed.

There is also, as we mentioned in the introduction, a class of time-based models of conditioning which base learning on prediction error (e.g. Mondragón et al., (2014); Sutton & Barto, 1990; Vogel Brandon & Wagner, 2003). Models of this type can anticipate the pattern

¹ The additional factor of target did not interact with the effects of interest, which showed the same pattern of significance as outlined above. See supplementary materials for complete analysis.

of results reported here, and may represent the best chance for associative theories to accommodate time-based characteristics of the conditioning process.

In summary, the present results provide further support for the proposal that associative learning can be influenced by the temporal distribution of the CS. Fixed duration CSs support a higher rate of conditioned responding than variable cues matched in mean duration (Jennings et al., 2013); they also produce better overshadowing (Bonardi et al., 2014) and in the present study better blocking. The models of conditioning and timing best equipped to explain these findings come from the class of hybrid models based on prediction-error learning in real time, such as the SSCC TD model proposed by Mondragón et al. (2014).

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Table 1: Design of Experiment 1. *F* and *Fc* were auditory stimuli of a fixed 10-s duration; *V* and *Vc* were variable-duration auditory stimuli with a mean duration of 10s; *X* and *Y* were visual stimuli either of fixed or variable duration (see text). *B* = Block, *O* = Overshadow; + denotes reinforcement, - nonreinforcement.

Group	Stage 1		Stage 2		Test
B	F+ Fc-	V+ Vc-	FX+ VY+		X? Y?
O	F- Fc+	V- Vc+	FX+ VY+		X? Y?

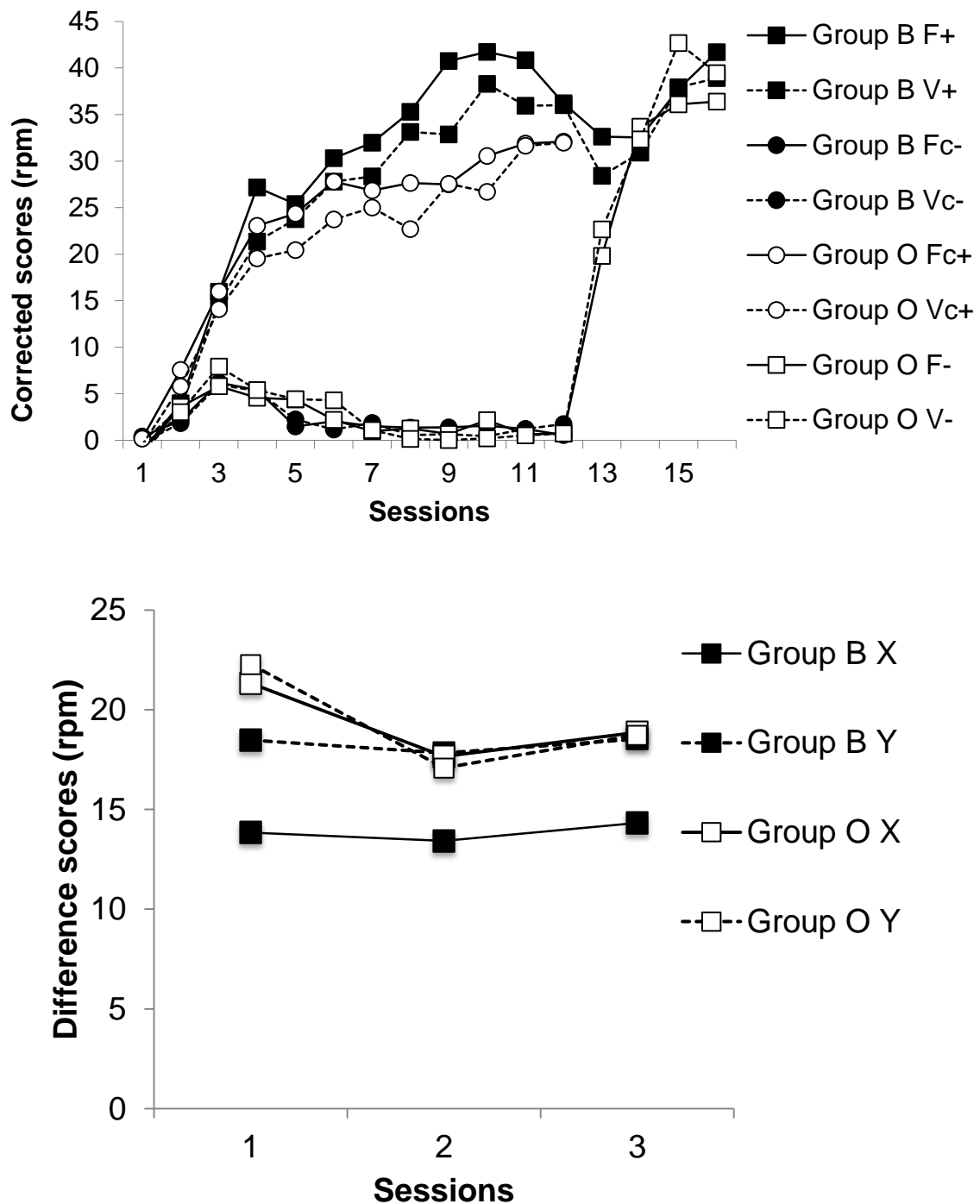


Figure 1 Group mean corrected response rates. Panel a: Scores during the reinforced and nonreinforced fixed- and variable-duration cues in Stage 1 (sessions 1-12) and Stage 2 (sessions 13-16; See Table 1). Panel b: Scores for X and Y for each session of the test.