

# Summation of reinforcement rates when conditioned stimuli are presented in compound

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## Abstract

Three experiments used delay conditioning of magazine approach in rats to examine the summation of responding when two conditioned stimuli (CSs) are presented together as a compound. The duration of each CS varied randomly from trial-to-trial around a mean that differed between the CSs. This meant that the rats' response rate to each CS was systematically related to the reinforcement rate of that CS, but remained steady as time elapsed during the CS (Harris & Carpenter, in press; Harris, Gharaei, & Pincham, in press). When the rats were presented with a compound of two CSs that had been conditioned separately, they responded more during the compound than during either of the CSs individually. More significantly, however, in all three experiments, the rats responded to the compound at the same rate as they responded to a third CS that had been reinforced at a rate equal to the sum of the reinforcement rates of the two CSs in compound. We discuss the implications of this finding for associative models (e.g., Rescorla & Wagner, 1972) and rate-based models (Gallistel & Gibbon, 2000) of conditioning.

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Running head: Summation of reinforcement rates

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Harris and Carpenter (in press) have recently reported a series of experiments that examined the relationship between the rate at which a conditioned stimulus (CS) is reinforced with an unconditioned stimulus (US) and the rate at which rats respond to the CS. A critical feature of these experiments was that the duration of each CS, and thus the CS-US interval, varied randomly from trial-to-trial within a uniform distribution. This meant that the rats' response rate,  $R$ , remained steady as time elapsed during presentations of the CS (Harris et al., in press). This contrasts with the typical pattern of responding observed with fixed duration CSs when responding gradually escalates across the CS-US interval and peaks close to the scheduled time of the US (Davis, Schlesinger, & Sorenson, 1989; Harris et al., in press; Kehoe & Joscelyne, 2005; Pavlov, 1927; Roberts, 1981; Smith, 1968; Williams, Lawson, Cook, Mather, & Johns, 2008). Thus, for fixed CSs,  $R$  varies as a function of both reinforcement rate,  $r$ , and reinforcement time (Harris, in press), making it impossible to isolate the relationship between  $r$  and  $R$ . For variable CSs, on the other hand, the relationship between  $R$  and time is more-or-less constant, making it possible to determine how  $R$  varies as a function of  $r$ .

To investigate the relationship between  $R$  and  $r$ , Harris and Carpenter (in press) trained rats in a magazine-approach paradigm with four variable CSs. The  $r$  differed between the four CSs, either by virtue of differences in the mean CS-US interval or differences in the proportion of trials that were reinforced with the US. In either case,  $R$  was a monotonic function of  $r$ , and was closely approximated by a hyperbolic function,  $R = Ar/(r+c)$ , where  $A$  is the asymptote of the function and  $c$  determines how quickly the function approaches that asymptote ( $R = \frac{1}{2}A$  when  $r = c$ ). Harris and Carpenter noted

that the relationship between  $R$  and  $r$  is consistent with two very different theoretical approaches to associative learning. According to one of these approaches, what is learned during conditioning consists of the formation of an excitatory link between the CS and US. The most popular version of this account views learning as the output of an error-correction algorithm that continuously updates the animal's knowledge of the CS-US association by changing the strength,  $V$ , of the CS-US link (Bush & Mosteller, 1951; Rescorla & Wagner, 1972). Computationally, on any trial when the CS and US are paired,  $V$  increases by a fixed proportion ( $k$ ) of the difference between the maximum ( $\lambda$ ) that can be learned about the CS-US association and the associative strength that has already been learned ( $V_{t-1}$ ). Thus, learning ( $\Delta V$ ) on trial  $t$  is defined as

$$\Delta V_t = k(\lambda - V_{t-1}) \quad \text{Equation 1}$$

This simple description of the trial-by-trial growth in  $V$  captures the increase in conditioned responding across trials in simple conditioning preparations (Harris, in press; Kehoe, Ludvig, Dudeney, Neufeld, & Sutton, 2008) (but see Gallistel, Fairhurst, & Balsam, 2004).

Rescorla and Wagner (1972) greatly extended the explanatory scope of this simple description by proposing that learning on any trial is proportional to the difference between  $\lambda$  and the sum of what has been learned about all CSs present on the current trial ( $\Sigma V$ ). Harris and Carpenter (in press) used this learning rule to derive the terminal  $V$  of a CS (the point at which, after sufficient training,  $V$  no longer changes from one trial to the next) as a function of its  $r$ . This analysis showed that the relationship between terminal  $V$  and  $r$  is closely approximated by a hyperbolic function. In other

words, the observed function relating  $R$  to  $r$  is predicted by the theoretical relationship between  $V$  and  $r$  derived from Equation 1.

The fact that both  $V$  and  $R$  are related to  $r$  by the same type of function means that we can, at least in the magazine approach paradigm, specify how  $V$  and  $R$  are related to each other, thereby allowing us to use  $R$  as a more precise measure of  $V$  than is typically accepted by most researchers. That is,  $V$  and  $R$  must share either a linear relationship,  $R = mV$ , or they must be related by a hyperbolic function,  $R = AV/(V+c)$ . If their relationship is linear,  $R$  can be used as a ratio scale of measurement of  $V$ . If they are related by a hyperbola, there is an affine (straight line) relationship between the inter-response interval,  $I$ , and  $1/V$ , such that  $I$  represents an interval scale of measurement of  $1/V$  (Harris & Carpenter, in press). (Note that, while both the linear and affine functions are straight lines, only the linear function passes through the origin, which is why it constitutes a ratio scale of measurement, whereas the affine function constitutes an interval scale of measurement.) In either case, response rate in magazine approach can be used as a more informative measure of  $V$  than is possible when relying on the common assumption that the scaling between  $V$  and performance is ordinal.

The other approach to learning that speaks directly to the findings reported by Harris and Carpenter (in press) eschews all notions of associative strength, and instead assumes that animals encode and remember the time intervals between events. One particularly prominent account of this type identifies the content of learning with rates of reinforcement. According to Rate Estimation Theory (RET, Gallistel & Gibbon, 2000), during conditioning animals learn about the rate at which USs occur

during a CS (the inverse of the cumulative CS-US interval) and the rate at which USs occur in the absence of the CS (the background rate of reinforcement). The decision to respond is based on a comparison between these rates of reinforcement, such that responding appears when the ratio of the rate expected during the CS and the background exceeds a threshold. Gallistel and Gibbon directly relate this decision process to the operations that are assumed to underlie the allocation of responding in reinforcement schedules, most famously characterized by Herrnstein's Matching Law. In this framework, the rate at which an animal makes a given response is determined by the rate at which that response is reinforced relative to reinforcement of all responses in that situation. This can be specified by the hyperbolic function,  $R_x = Ar_x/(r_x+r_o)$ , where  $r_x$  and  $r_o$  are the reinforcement rates of the target behavior and other behaviors, respectively. Therefore, this approach also specifically predicts the observations made by Harris and Carpenter. In this case,  $R$  bears a hyperbolic relationship to what is learned about a CS, and the content of that learning is directly (linearly) related to  $r$ .

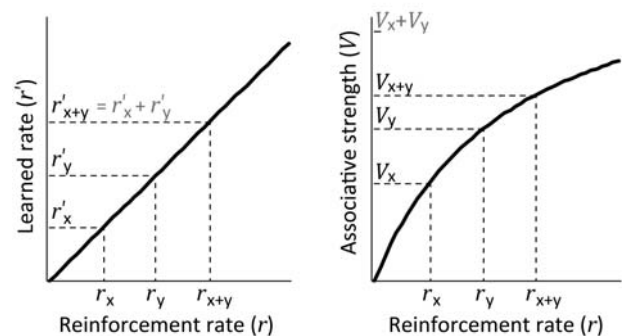
While both approaches described above can account for the hyperbolic relationship between  $r$  and  $R$  observed by Harris and Carpenter (in press), the models differ markedly in their descriptions of the content of what is learned during conditioning and how that content is related to  $r$ . As noted, according to associative models (e.g., Rescorla & Wagner, 1972), the content of learning is  $V$  which is related to  $r$  by a hyperbolic function, whereas a model like RET (Gallistel & Gibbon, 2000) assumes that reinforcement rate is the content of learning, and thus learning is a linear function of  $r$ . These differences between the two accounts can be

### Summation of reinforcement rates.

used to generate empirically distinct predictions. One testable prediction stems from the assumption, common to both the Rescorla-Wagner model and RET, that what is learned about two CSs will combine additively when those CSs are presented together as a compound. That is, when two separately trained CSs, A and B, are presented as the compound AB, the Rescorla-Wagner model predicts that  $V_{AB} = V_A + V_B$ , and RET predicts that  $r'_{AB} = r'_A + r'_B$  (where  $r'$  is the animal's learned estimate of  $r$ ). It follows that, according to RET, the response to AB will be the same as the response to a third CS, X, that has been reinforced at a rate equalling the sum of the rates of A and B. This specific prediction depends upon there being a linear relationship between  $r$  and learning, because only this relationship preserves the additivity between the learned rates and the actual reinforcement rates. Therefore, the prediction is different for any model which assumes a non-linear relationship between learning and  $r$ , and in the case of the Rescorla-Wagner model, the hyperbolic relationship between  $V$  and  $r$  means that  $V_A + V_B > V_X$  if  $r_X = r_A + r_B$ . Figure 1 shows graphically how the different predictions are derived for the two classes of model.

There are numerous experiments showing that responding to a compound is greater than responding to the individual CSs that make up the compound (e.g., Kehoe, 1982; Kehoe, 1986; Rescorla, 1997; Thein, Westbrook, & Harris, 2008), consistent with the principle of summation. However, none of these experiments provides meaningful information with which to estimate the amount of summation that occurred or whether this summation was closer to what would be predicted based on summation of  $V$ s or summation of  $r$ s. This was the aim of the

current experiments which investigated summation of magazine approach responding in rats. In all experiments, rats were first trained with two variable CSs, A and B, before they were tested with the compound AB. The  $R$  to AB was compared with that to another CS, X (or compound, XY), that had been reinforced at a rate equal to the sum of the  $r$ s of A and B (i.e.,  $r_X = r_A + r_B$ ). As explained above, if rats learn directly about  $r$  during conditioning, as is assumed by RET, then  $R_{AB}$  should equal  $R_X$ . However, if rats learn about  $V$  during conditioning, as computed in Equation 1, then  $R_{AB}$  should be greater than  $R_X$  because  $V_{AB} = V_A + V_B > V_X$ . Note that these predictions do not depend on specific assumptions about the relationship between  $R$  and  $V$  (or between  $R$  and  $r'$ ), as long as the function is monotonically increasing.



**Figure 1. Left:** A linear function between learned reinforcement rate ( $r'$ ) and actual reinforcement rate ( $r$ ), as assumed by conditioning models in which animals encode and remember  $r$ s (e.g., Gallistel & Gibbon, 2000). The linear relationship means that the sum of any two  $r$ s is preserved in the sum of the  $r'$ s. **Right:** An hyperbolic function between associative strength ( $V$ ) and  $r$ , as assumed by associative models based on an error-term learning rule (e.g., Rescorla & Wagner, 1972). The nonlinear nature of the relationship between  $V$  and  $r$  means that the sum of any two  $r$ s is not preserved in the sum of their  $V$ s. In the example shown here, a reinforcement rate of  $r_{x+y}$  produces an associative strength  $V_{x+y}$  that is less than  $V_x + V_y$ .

## Experiment 1

The first experiment aimed to investigate summation when two CSs are separately conditioned then tested as a compound. In a fully within-subjects design, the experiment trained rats with two single CSs, A and B, as well as a compound, XY. On any given trial, termination of the CSs or compound was immediately followed by delivery of a food pellet (US). Once magazine responding reached a stable level, the rats were given two “probe” tests per session with the compound AB<sup>1</sup>. The duration of each CS or compound presentation varied between trials to prevent the rats from tracking the fixed timing of the US (Harris et al., in press). The durations of the two CSs were sampled randomly from uniform distributions, one (A) with a mean of 50 s, the other (B) with a mean of 75 s. The duration of the compound, XY, had a mean of 30 s. Therefore,  $r_{XY} = r_A + r_B$  (i.e.,  $1/30 = 1/50 + 1/75$ ). According to RET,  $r'_{AB} = r'_A + r'_B = r'_{XY}$ , and so  $R_{AB}$  should equal  $R_{XY}$ . According to the Rescorla-Wagner (1972) model,  $R_{AB}$  should be greater than  $R_{XY}$  because  $V_{AB} > V_{XY}$ .

Data from all experiments presented in this paper can be downloaded from the website: <http://sydney.edu.au/science/psychology/staff/justinh/downloads/>

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<sup>1</sup> We waited until responding to each CS was close to its asymptote before starting probe tests because this maximized the separation of  $R$ s between the CSs. We note, however, that the current predictions of the Rescorla-Wagner (1972) model do not depend on  $R$ s being at asymptote since, across acquisition, the  $V$ s for each CS should increase in fixed proportion to one another.

## Method

### *Subjects*

Sixteen, experimentally naïve male Hooded Wistar rats (*Rattus Norvegicus*) were obtained from the Laboratory Animal Services breeding unit at the University of Adelaide, South Australia. They were 113 days old at the beginning of the experiment and had a mean body weight of 400 g. They were housed in groups of 8 in white plastic tubs (26cm in height, 59cm in length and 37cm in depth), with free access to water throughout the experiment. Over the 3 days before the experiment, their access to food was progressively reduced and for the duration of the experiment, daily food access was restricted to a 2-hr period immediately after testing.

### *Apparatus*

Rats were conditioned in 16 Med Associates (St Albans, VT) chambers measuring 28.5cm in height, 30cm in length and 25cm in depth. The two end walls in each chamber were made of aluminum and the sidewalls and ceiling were made of Plexiglas. The chamber floors were 0.5 cm diameter stainless steel rods spaced 1.5cm apart. A recessed food magazine was located in the middle of one end wall in each chamber. A 3.5 cm diameter, 0.5cm deep metal dish was fixed to the floor of each food magazine. An infrared photo-beam that spanned the entrance to the magazine was used to record each time the rat poked its head into the magazine. A dispenser containing 45mg pellets (Noyes, Formula P; Research Diets Inc, New Brunswick, NJ) was attached to the food magazine. A speaker emitting the white noise stimulus, measuring approximately 78dB, was attached to the wall to the right and above the magazine.

## Summation of reinforcement rates.

All chambers were enclosed in a sound-restricted, light-resistant wooden shell. Fans located in the rear wall provided ventilation; the operation of these created a background level of noise measuring 70dB. White noise (78dB) was presented from a speaker mounted on the wall of each operant chamber above and to the right of the food magazine. A tone (78dB and 2.9 kHz) was produced from a piezo buzzer positioned on the floor of the sound-attenuating shell behind each operant chamber. A grid of white LED lights (30cd/m<sup>2</sup>) was located in front of the chamber on the floor of the shell – these LEDs were capable of being flashed at 2Hz to present a flashing light stimulus. An incandescent house light was located on the rear wall of the shell, capable of being illuminated at 30 cd/m<sup>2</sup> as a steady light stimulus during the session, which was otherwise dark. Computers located in the same room controlled and recorded all experimental events automatically. The computer registered and recorded each photobeam break (nose pokes as the rat's head entered the magazine) during the presentation of the CS. To ascertain a baseline measure of the response rate, the computer also recorded the number of magazine entries during the 30-s period immediately before the onset of the CS on each trial.

### *Procedure*

The rats received 20-min magazine training sessions on each of two days, in which 20 food pellets were delivered on a variable time (VT) 1-min schedule. Two rats received an extra 2 sessions on the third day as they failed to eat any of the food in the magazine in the first 2 sessions. Over the next 50 days, the rats received 10 presentations per day of each of three trial types. A compound (XY) comprised

of an auditory and a visual stimulus was presented for a variable duration taken from a uniform distribution with a mean of 30 s and a range of 2 s to 58 s. Two single CSs, one auditory one visual, were also presented for variable durations taken from a uniform distribution with a mean of 50 s (CS A: range 2 s to 98 s) or a mean of 75 s (CS B: range 2 s to 148 s). The allocation of stimuli (tone, white noise, flash, and light) as the compound XY and CSs A and B was counterbalanced across rats with the constraint that X and Y always belonged to different modalities (one auditory, the other visual), as did A and B. The average inter-stimulus-interval was 120 s (the intervals varied randomly according to a uniform distribution, but with a minimum of 32 s). On every trial, the termination of the CS or compound coincided with delivery of a single food pellet. Across all 50 days, the timing of each photo-beam interruption by head entry into the magazine was recorded during each trial and each 30-s pre-CS period.

For the last 15 sessions (Days 36-50), two additional probe trials of the compound AB were introduced into each experimental session. These occurred at different times across days, but never within the first four or last three trials of the session. The probe presentations had a fixed 30-s duration, and were reinforced with a food pellet. The test sessions also included two 30-s probe trials of each of X and Y presented separately, however, we have not presented these data for two reasons. First, responding during X and Y probe trials increased across the test sessions, suggesting that the rats began to learn that X and Y were each reinforced at a relatively high rate of 1/30 s (higher than would be expected given that the XY compound was reinforced at that rate). Second, we realised with hindsight

## Summation of reinforcement rates.

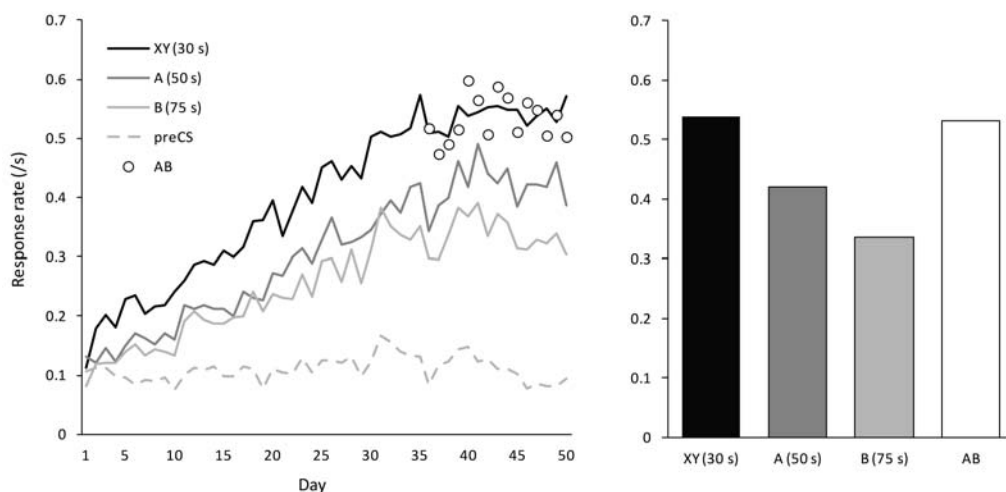
that the experiment did not include an appropriate comparison CS against which we could assess how much had been learned about X and Y individually. We are currently pursuing this issue in a separate series of experiments.

### Results and Discussion

The left side of Figure 2 plots  $R$  during the compound, XY, and during each of the single CSs, A and B, across all 50 days of Experiment 1.  $R$ s increased slowly over the first 35 days, and remained relatively steady thereafter. A repeated measures ANOVA, with Greenhouse-Geisser correction when necessary, was used to analyse  $R$ s during XY, A and B. This revealed significant main effects of stimulus,  $F(1.1,17.1) = 48.63$ ,  $p < .001$ , and of Day,  $F(3.0,44) = 14.98$ ,  $p < .001$ , and a significant interaction between stimulus and Day,  $F(8.3,124) = 5.06$ ,  $p < .001$ .

From Day 36 to Day 50, each session included two probe trials with the compound AB. Response rates during these probes are

shown as white circles in the plot on the left side of Figure 2. While responding during these probe trials varied from one day to the next, there was no systematic trend for response rates to change across days, suggesting that there was little additional learning during these trials. The right side of Figure 2 shows  $R$ s during probe trials, and during presentations of A, B, and XY, averaged over the last 15 days. The key analysis compares responding to AB with the trained stimuli. To limit the number of separate comparisons, we confined this analysis to just two paired  $t$ -tests that compared AB with A and XY. The significance level was adjusted to .025. This analysis shows that  $R$  during the compound AB was significantly higher than during A,  $t(15) = 5.26$ ,  $p < .001$ . However,  $R$  during AB was not significantly different from  $R$  during XY,  $t(15) < 1$ . Indeed, as can be seen in Figure 2, these were almost identical: mean  $R_{XY} = .54$ , and mean  $R_{AB} = .53$ . We note that the close match between  $R_{XY}$  and  $R_{AB}$  was also evident on the very first probe test on Day 36 (see left panel of Figure 2), before any possibility that responding



**Figure 2.** **Left:** Mean response rates (responses per second) to the compound, XY, and two single CSs, A and B, on each day of Experiment 1. The duration of each stimulus varied from trial-to-trial around a mean of 30 s (XY), 50 s (A), or 75 s (B). On Days 36 to 50, each session included probe trials of the compound AB. **Right:** Response rates to XY, A, B, and AB, averaged over the final 15 days.

to AB had been affected by reinforcement on those probe trials. This result is precisely what is predicted by RET (Gallistel & Gibbon, 2000) which assumes that animals learn specifically about  $r$  and their estimate of  $r$  ( $r'$ ) during a compound of two CSs is the sum of  $r'$  of each individual CS. The present findings do not support associative models (e.g., Rescorla & Wagner, 1972) which assume that what is learned,  $V$ , is not linearly related to  $r$ , and thus the sum of what is learned about two CSs will not equal the sum of their  $rs$ .

The evidence offered here in favor of RET (Gallistel & Gibbon, 2000) over associative models rests on findings that support a null hypothesis, that  $R_{AB} = R_{XY}$ , rather than an alternative hypothesis that  $R_{AB} > R_{XY}$ . While the  $t$ -tests used above do not provide a basis on which to reject the alternative in favor of the null, these hypotheses can be compared using a Bayesian analysis, as recently described by Gallistel (2009). Given that the means of  $R_{AB}$  and  $R_{XY}$  are very close, it should not be surprising that the likelihood function for the mean difference between  $R_{AB}$  and  $R_{XY}$  across all 16 rats is centred very close to zero. (In calculating this likelihood function, we have assumed that the difference scores are normally distributed with  $\sigma = 0.088$ , as the unbiased estimate of the standard deviation of the data.) The likelihood of the alternative hypothesis, that  $R_{AB} > R_{XY}$ , depends on how precise we can be in specifying the size of this difference. According to the Rescorla-Wagner (1972) model, the associative strength of AB will equal  $[V_A + V_B]$ , but our prediction for  $R_{AB}$  will depend on how well we can define the relationship between  $R$  and  $V$ . Harris and Carpenter (in press) showed that, in this paradigm, the relationship between  $R$  and  $V$  is either linear or a hyperbolic function similar to that shown on

the right of Figure 1. If the relationship is linear, the prediction for  $R_{AB}$  is that it will equal  $[R_A + R_B]$ . In this case, the ratio of the marginal likelihoods of the null hypothesis and this alternative hypothesis gives us odds favoring the null hypothesis (i.e., RET over Rescorla-Wagner) of more than 1000:1. However, if the relationship between  $V$  and  $R$  is hyperbolic, then  $R_{AB} < R_A + R_B$ , in which case  $[R_A + R_B]$  becomes the upper limit on the prediction for  $R_{AB}$ . Since the lower limit of  $R_{AB}$  is given by  $R_{XY}$  (because  $R_{AB}$  must be greater than  $R_{XY}$ ), the Rescorla-Wagner model is constrained to predict that  $R_{AB}$  will fall within the range from  $R_{XY}$  to  $[R_A + R_B]$ . Based on the ratio of the marginal likelihoods of the null hypothesis and this particular alternative hypothesis, the odds favoring the null hypothesis are 9:1.

## Experiment 2

Experiment 1 compared the  $R$  to a compound, AB, composed of two CSs that had been reinforced at rates of 1/50 s and 1/75 s, with  $R$  to a second compound, XY, that had been reinforced at 1/30 s. The rats responded at the same rate to AB and XY, suggesting that they had learned about the  $r$  of A and B, and this learning about each CS was summed when A and B were combined as a compound. However, there are two other factors that may have influenced the rats' responses to AB in Experiment 1 and thus complicate the interpretation of those results. First, it is possible that  $R$ s to AB and XY were close to a response ceiling which would have obscured any difference between the two compounds. Second, it is possible that the rats' responses to AB were influenced by generalisation from XY, given their similarity as audiovisual compounds. Indeed, Pearce, George and Aydin (2002) have



provided evidence for such an influence of one compound on another in experiments designed to investigate summation between CSs.

Experiment 2 was designed to address the two issues raised above. Rats were trained with four single CSs, each at a different  $r$ . The mean CS-US intervals were 30 s (A), 50 s (B), 75 s (C), and 150 s (D).  $R$ s during the compounds BC and CD were then compared with  $R$ s during the single CSs. The comparisons of interest were between BC and A, because  $r_A = r_B + r_C$ , and between CD and B, because  $r_B = r_C + r_D$ . One important aspect of this experiment is that the rats were not trained with any compound stimuli, and therefore there would be no opportunity for generalization from a trained compound to influence responding to the test compounds. Further, the design of Experiment 2 allowed us to assess simultaneously summation in two compounds that should evoke different levels of responding. If  $R_{BC} = R_A$  and  $R_{CD} = R_B$ , despite differences between  $R_{BC}$  and  $R_{CD}$ , this would replicate the key finding of Experiment 1 while discounting the possibility of a loss of sensitivity in the relevant regions of the response scale that might be caused, for example, by a ceiling effect.

## Method

### *Subjects and apparatus*

Sixteen experimentally naïve male Hooded Wistar rats were obtained from the same source, and housed in the same manner, as in Experiment 1. They were 50 days old and had a mean body weight of 260 g at the start of the experiment. Their daily access to food was restricted to a 2-hr period immediately after testing. They were trained in the same 16

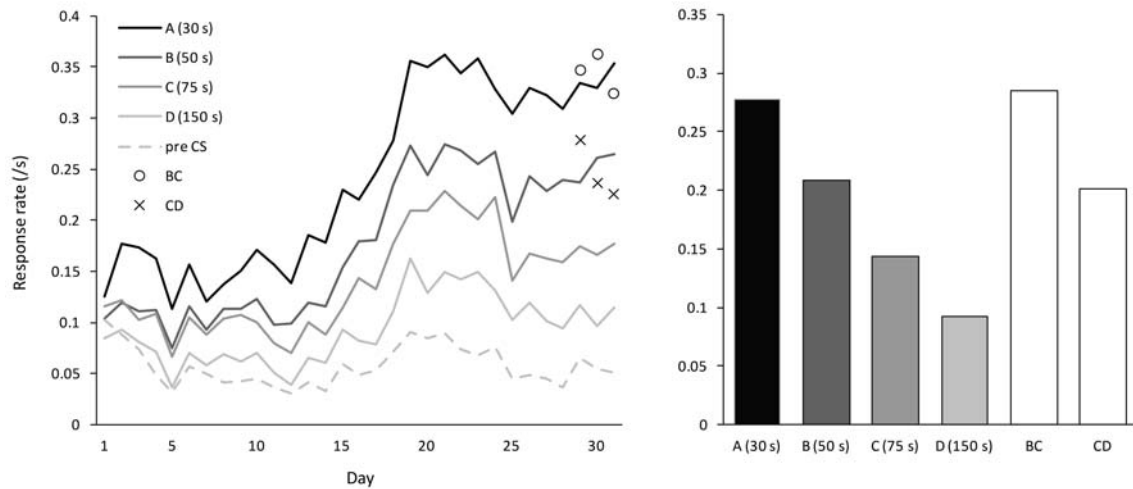
chambers, with the same 4 counterbalanced stimuli, as in Experiment 1.

### *Procedure*

The rats received one 20-min magazine training session in which 20 food pellets were delivered on a VT 1-min schedule. Over the next 31 days, they received 12 presentations per day of each of four variable duration CSs: A was presented for a mean of 30 s (2 to 58 s); B for a mean of 50 s (2 to 98 s); C for a mean of 75 s (2 to 148 s); and D for a mean of 150 s (2 to 298 s). All CS presentations ended with the delivery of a food pellet. The physical identities of the four stimuli were counterbalanced with the constraint that A and C always belonged to one modality (auditory or visual) and B and D to the other (visual or auditory) so that compounds BC and CD contained one auditory and one visual stimulus. As in Experiment 1, the average inter-trial interval was 120 s, and all interruptions of the photo-beam by head entry into the magazine were recorded during the CSs and pre-CS period.

Starting on Day 29, two reinforced probe trials of each compound BC and CD were added into each experimental session. These occurred on different trials across days and across rats, but never occurred earlier than trial 8 or later than trial 46 (of 52), and were spaced roughly 10 trials apart. One probe trial of each compound type occurred in each half of the session. These presentations were 50 s and 75 s for BC, and were 75 s and 150 s for CD, thus matching the mean durations of the CSs from which they were composed. This was continued for 3 sessions. The experiment could not be continued beyond this point due to external factors.

### Summation of reinforcement rates.



**Figure 3.** **Left:** Mean response rates (responses per second) to each of the four trained CS (A, B, C, and D) on each day of Experiment 2. CS durations varied from trial-to-trial around a mean of 30 s (A), 50 s (B), 75 s (C), or 150 s (D). On Days 29 to 31, each session included probe trials of the compounds BC and CD. **Right:** Response rates to the four trained CSs and the probe compounds, averaged over the final 3 days.

### Results and Discussion

*R*s to the four single CSs across each day of Experiment 2 are plotted on the left side of Figure 3. These increased over the first 20 days of training, but changed little thereafter. Thus responding had reached an asymptote after fewer sessions in this experiment than in Experiment 1, possibly because the rats were younger and there were more trials per session in this than in the previous experiment. It is clear that, at this point, the rats responded differentially to the four CSs, and *R* was a uniform function of the *r* of each CS. A repeated measures ANOVA, analysing *R*s during each CS across days, revealed significant main effects of stimulus,  $F(1.5,22) = 17.21$ ,  $p < .001$ , and of Day,  $F(2.7,41) = 7.98$ ,  $p < .001$ , and a significant interaction between stimulus and Day,  $F(6.2,94) = 4.85$ ,  $p < .001$ .

We commenced probe tests with the compounds BC and CD on Day 29. Response rates during these probes are shown as white circles in the plot on the left side of Figure 3.

Responding during these probe trials was relatively constant across days, suggesting that there was little additional learning during these trials. The *R* to each CS and to both compounds, averaged over the last three days of the experiment, is shown on the right side of Figure 3. The critical analysis compares *R*s between the test compounds and the single CSs. To reduce the number of separate comparisons, and thus the correction to alpha, we confined the analysis to five paired *t*-tests that compared each compound to the higher of its two constituent CSs and to the CS with *r* equal to the summed *r* of the compound, as well as comparing the two compounds against each other. For this set of comparisons, the significance level was adjusted to .01. The analysis revealed that responding to BC was significantly greater than to B,  $t(15) = 3.34$ ,  $p = .004$ , but did not differ from responding to A,  $t(15) < 1$ . Indeed, the rats responded to BC at almost exactly the same level as to A: mean  $R_{BC} = .28$ , mean  $R_A = .28$ . The analysis also revealed that the difference in *R* between CD and C was at the significance threshold,  $t(15) = 2.92$ ,  $p =$

.010. The  $R_s$  did not differ between CD and B,  $t(15) < 1$ , and once again these values were almost identical: mean  $R_{CD} = .20$ , mean  $R_B = .21$ . Finally,  $R_s$  to BC and CD were significantly different from each other,  $t(15) = 3.14$ ,  $p = .007$ , confirming that the rats did discriminate between the two test compounds.

We have again performed a Bayesian analysis (Gallistel, 2009) to compare the null hypotheses, that  $R_{BC} = R_A$ , and  $R_{CD} = R_B$ , with alternative hypotheses from the Rescorla-Wagner (1972) model, that  $R_{BC} > R_A$ , and  $R_{CD} > R_B$ . Given the means of  $R_A$ ,  $R_{BC}$ ,  $R_B$  and  $R_{CD}$  reported above, it should not be surprising that the likelihood functions for the mean differences between  $R_{BC}$  and  $R_A$ , and between  $R_{CD}$  and  $R_B$ , are centered very close to zero. (As for Experiment 1, in calculating these likelihood functions, we have assumed that the difference scores are normally distributed with  $\sigma = 0.152$  and  $0.049$ , as the unbiased estimates of the standard deviation of the differences between  $R_{BC}$  and  $R_A$ , and between  $R_{CD}$  and  $R_B$ , respectively.) In testing the likelihood of the Rescorla-Wagner model's predictions, if we assume there to be a linear relationship between  $V$  and  $R$ , such that  $R_{AB} = R_A + R_B$ , and  $R_{CD} = R_C + R_D$ , the ratios of the marginal likelihoods of the null hypotheses and these alternative hypotheses give us odds favoring of the null hypotheses for each compound, with odds of nearly 5:1 for BC, and 38:1 for CD. If, instead, we assume there to be a hyperbolic relationship between  $V$  and  $R$ , we can no longer give exact predictions for  $R_{BC}$  or  $R_{CD}$ , but we can specify a range within which the predicted values will fall: for  $R_{BC}$  this range will be between  $R_A$  and  $[R_B + R_C]$ ; for  $R_{CD}$  the range will be between  $R_B$  and  $[R_C + R_D]$ . Based on the ratios of the marginal likelihoods of the null hypotheses and these vaguer alternative

hypotheses, the odds still favor the null hypothesis for both  $R_{BC}$  and  $R_{CD}$  (1.4:1 and 2.5:1, respectively).

Experiment 2 has confirmed the key finding from Experiment 1: when rats are presented with a compound of two CSs, their response to the compound is almost perfectly predicted by the sum of the  $r_s$  of the individual CSs. This result was simultaneously observed with two different compounds, at different levels of responding, and thus comparisons of the rats'  $R_s$  were not confounded by a possible loss in sensitivity of the response scale (such as a ceiling effect).

### Experiment 3

In Experiments 1 and 2, rats responded to a compound of two CSs (e.g., A and B) at the same level as they responded to another CS or compound that had been reinforced at a rate equal to the sum of the  $r_s$  of A and B. In both of those experiments,  $r$  varied between CSs as a function of their mean CS-US interval. Experiment 3 also investigated summation of responding between CSs, but the  $r$  of each CS was manipulated by varying the proportion of trials that were reinforced with the US. Thus in this experiment, all CSs had the same mean duration of 10 s. One CS, A, was reinforced on 100% of trials. A second CS, B, was reinforced on 33% of trials, and two other CSs, C and D, were each reinforced on 17% of trials. Once responding to these CSs reached a steady rate, we presented probe trials of the compound CD. If rats learn about the  $r$  of each CS during training, and if they sum together what they have learned about two CSs when those CSs are presented as a compound, then we expect that  $R$  during CD should equal  $R$  during B, because  $r_B$

$= r_C + r_D$ . Responding to B and CD should be less than responding to A, which would confirm that the  $R$  for B and CD was not affected by a response ceiling.

## Method

### *Subjects and apparatus*

Sixteen experimentally naïve male Hooded Wistar rats were obtained from the same source, and housed in the same manner, as in Experiment 1. They were 53 days old and had a mean body weight of 175 g at the start of the experiment. Their access to food was restricted to a 2-hr period immediately after testing. They were trained in the same 16 chambers, with the same 4 counterbalanced stimuli, as in Experiment 1.

### *Procedure*

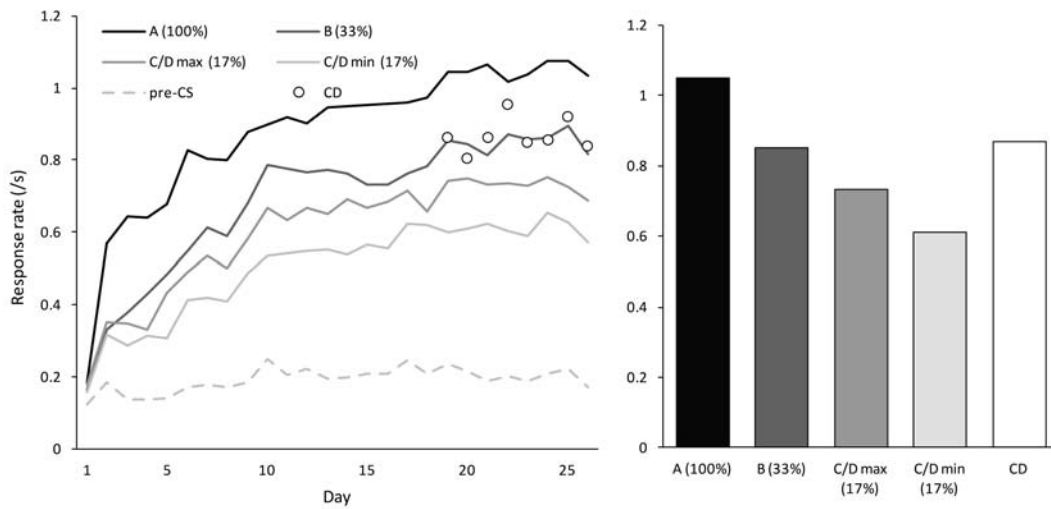
The rats received one 20-min magazine training session in which 20 food pellets were delivered on a VT 1-min schedule. On each of the next 26 days, four variable-duration CSs were presented 18 times each (a total of 72 trials per day). The mean duration of each CS was 10 s (range 2 to 18 s), and mean inter-trial interval was 120 s. One CS, A, was followed by delivery of a food pellet on all 18 trials. CS B was followed by food on 6 of the 18 trials (33%). CSs C and D were followed by food on 3 of the 18 trials (17%). The physical identities of the four stimuli were counterbalanced with the constraint that C and D always belonged to different modalities. Starting on Day 19, two probe trials of compound CD were inserted into each experimental session at Trials 24 and 48 (of 74). These presentations had a fixed duration of 10 s, and were never reinforced with food. This was continued for 8 sessions.

## Results and Discussion

The  $R$ s to each CS across the 26 days of Experiment 3 are shown on the left side of Figure 4. Responding appeared to reach a stable level after 18 days of conditioning. It is likely that near-asymptotic responding was reached earlier than in either of the previous two experiments because there were many more trials per day in this experiment. For each rat, we calculated which CS, of C and D, elicited more responding averaged over the 26 days, and on this basis we distinguished between “C/D max” and “C/D min” CSs. A repeated measures ANOVA conducted on responding to all four CSs confirmed that there were significant main effects of stimulus,  $F(1.6,24.2) = 27.79$ ,  $p < .001$ , and Day,  $F(3.0,45) = 20.22$ ,  $p < .001$ . The interaction between these factors fell just short of statistical significance,  $F(7.3,109) = 2.00$ ,  $p = .059$ .

The data of primary interest is from Days 19 to 26, which included probe trials with the compound CD. Response rates during these probes are shown as white circles in the plot on the left side of Figure 4. There was no systematic trend for a change in responding during these probe trials constant across days, suggesting that there was little additional learning during these trials.  $R$ s averaged over these 8 days are shown on the right side of Figure 4. We analysed these data using three paired  $t$ -tests that compared CD against A, B, and C/D max; the significance level was adjusted to .017. These analyses revealed that responding to CD was significantly greater than C/D max,  $t(15) = 2.73$ ,  $p = .016$ . The difference between CD and A fell just short of the adjusted significance level,  $t(15) = 2.64$ ,  $p = .019$ . Of most importance, the  $R$  during CD did not differ from the  $R$  during B,  $t < 1$ , and indeed the value

### Summation of reinforcement rates.



**Figure 4.** **Left:** Mean response rates (responses per second) to each of the four trained CS (A, B, C/D max, and C/D min) on each day of Experiment 3. The durations of all 4 CSs varied around a mean of 10 s. The CSs differed in the proportion of trials that were reinforced: 100% (A), 33% (B), or 17% (C and D). For data presentation and analyses, we have identified which of the latter two CSs elicited the greater amount of responding (C/D max) and which the lesser amount of responding (C/D min). On Days 19 to 26, each session included probe trials of the compound CD. **Right:** Response rates to the four trained CSs and the probe compound, averaged over the final 8 days.

of these  $R$ s were very close: mean  $R_{CD} = 0.87$ , mean  $R_B = 0.85$ . This similarity between  $R_{CD}$  and  $R_B$  was evident from the very first probe test, before there was any opportunity for the rats to learn about the reinforcement rate of CD.

As for Experiments 1 and 2, we have performed a Bayesian analysis (Gallistel, 2009) to compare the null hypothesis, that  $R_{CD} = R_B$ , with the alternative hypothesis from the Rescorla-Wagner (1972) model that  $R_{CD} > R_B$ . The likelihood function for the mean difference between  $R_{CD}$  and  $R_B$  is centred very close to zero, as to be expected given how close their means are. (As for Experiment 1, we have assumed that the difference scores are normally distributed with  $\sigma = 0.152$ , as the unbiased estimates of the standard deviation of the differences between  $R_{CD}$  and  $R_B$ .) If we assume there to be a linear relationship between  $V$  and  $R$ , we can give an exact prediction for  $R_{CD}$ , namely that it will be equal to  $[R_C + R_D]$ . Based

on the ratio of the marginal likelihoods of the null and this alternative hypothesis, the odds favoring the null hypothesis are more than 1000:1. If, instead, we assume there to be a hyperbolic relationship between  $V$  and  $R$ , we can no longer give an exact prediction for  $R_{CD}$ , but we can specify that the value should fall within the range between  $R_B$  and  $[R_C + R_D]$ . Based on the ratio of the marginal likelihoods of the null and this particular alternative hypothesis, the odds still favor the null hypothesis 6.5:1. Thus these results again confirm the prediction of RET (Gallistel & Gibbon, 2000) that rats respond to a compound of two CSs at the same level as they respond to a CS that had been reinforced at a rate equal to the sum of the rates of reinforcement of the CSs in the compound.

### General Discussion

We have described three experiments that investigated summation of responding when two separately-conditioned stimuli are presented together as a compound. There are numerous studies that report evidence for summation, in that animals responded more during a compound than during either of the CSs from which it was composed (e.g., Kehoe, 1982; Kehoe, 1986; Rescorla, 1997; Thein et al., 2008). The present experiments go beyond those previous demonstrations by quantifying the amount of summation that occurs. This was achieved in the present experiments using CSs with randomly varying durations, whereas previous investigations of summation used fixed-duration CSs. The advantage conferred by variable CSs is that, at least in the present paradigm, rats respond at a steady rate across the duration of the CS (Harris et al., in press). Thus, unlike experiments that used fixed CSs, the rats' response rates,  $R$ , in the present experiments did not vary as a function of time, making it possible to isolate the relationship between  $R$  and reinforcement rate,  $r$ . In so doing, the present experiments consistently demonstrated that  $R$  to a compound of two CSs could be perfectly predicted by the sum of the  $r$ s of those CSs. That is, when CSs A and B had been reinforced at rates  $r_A$  and  $r_B$ , rats responded to the compound AB at exactly the same rate as they responded to a third CS that had been reinforced at a rate equal to  $r_A + r_B$ . This was demonstrated with four different compounds, and the same result was observed independently of where the compound was located on the response scale or how  $r$  was manipulated (by manipulating the mean CS-US interval, or the proportion of trials reinforced with food).

The present findings constitute clear support for any model, such as RET (Gallistel & Gibbon, 2000), which assumes that the content of what animals learn during conditioning is the rate at which the US occurs during the CS. In addition to this assumption, RET also assumes that an animal's estimation of  $r$  during a compound of two CSs is equal to the sum of  $r$ s of the CSs. This means that, according to RET, the animal's response to a compound can be predicted from the summed  $r$ s of the CSs. This is precisely what we have observed here.

The implications of the present findings for associative models depend on the rules that define the relationship between  $V$  and  $r$ , and how the  $V$ s of individual CSs are combined in compound. In the Introduction, we described at length these rules for the Rescorla-Wagner (1972) model. In short, the learning rule used by the model (Equation 1) predicts that the relationship between  $V$  and  $r$  is hyperbolic, which means that if  $r_X = r_A + r_B$ , then  $V_X < V_A + V_B$  (See Figure 1). Since the Rescorla-Wagner model also assumes simple summation of  $V$ s between CSs presented in compound, i.e.  $V_{AB} = V_A + V_B$ , it follows that  $V_{AB} > V_X$ . In other words, the Rescorla-Wagner model predicts that responding to a compound, AB, will be greater than responding to a CS, X, if  $r_X = r_A + r_B$ . Clearly this prediction is not supported by the present data which consistently show that  $R_{AB} = R_X$ . Further, we used a Bayesian analysis (Gallistel, 2009) to compare the likelihood that  $R_{AB} = R_X$  with the likelihood that  $R_{AB} \geq R_X$ . (Note that, by defining the second hypothesis as  $R_{AB} \geq R_X$ , we allowed it to include the possibility, specified in the first hypothesis, that  $R_{AB} = R_X$ .) For the data from each experiment, we found that the likelihood of  $R_{AB} = R_X$  was greater than likelihood of  $R_{AB} \geq R_X$ .

While the findings reported here are problematic for the Rescorla-Wagner (1972) model, they may appear less so for numerous other associative models (Harris, 2006; McLaren & Mackintosh, 2002; Pearce, 1994; Wagner, 2003; Wagner & Brandon, 2001), even though these models use the same learning rule defined in Equation 1. These more recent models all contain elaborated descriptions of how stimuli are represented within the learning mechanism, and in particular they invoke non-linear rules to account for generalisation of  $V$  between individual CSs and their compounds. As mentioned already, the Rescorla-Wagner model makes the very simple assumption that  $V$ s sum, such that  $V_{AB} = V_A + V_B$ . In contrast, each of the associative models listed above allows  $V_{AB}$  to be less than  $[V_A + V_B]$ , by virtue of a generalisation decrement between the individual CSs and their compound. In each case, the size of the decrement, and thus the difference between  $V_{AB}$  and  $[V_A + V_B]$ , can vary depending on factors such as the salience of the CSs versus the context, and the degree of similarity between the CSs. Indeed, in one of these models (Wagner, 2003; Wagner & Brandon, 2001), the amount of generalisation is set by a parameter that permits anything from complete summation,  $V_{AB} = V_A + V_B$ , to a complete failure of generalisation between CSs and their compound,  $V_{AB} = 0$ . As such, these more recent associative models tend to avoid making empirically-testable predictions about the amount of summation that will occur between CSs. This may seem to save those models from falsification by the present data, but only at a cost to their utility. Indeed, the Bayesian analysis we have used to test the predictions of the Rescorla-Wagner model would also penalise these models heavily for the lack of precision in their predictions. In effect, the analysis takes account of the fact

that, when a given result is consistent with the predictions of two models, the model that was more specific in predicting that result is more likely given the evidence than the model that only vaguely predicted the same result. Thus, the very specific (and thus highly falsifiable) predictions made by RET (Gallistel & Gibbon, 2000) are more likely given the present data than any loose set of predictions offered by alternative models.

In sum, the three experiments reported here have consistently shown that when rats were presented with a compound of two separately conditioned stimuli, A and B, their response to the compound could be accurately predicted from the sum of the rates at which A and B were reinforced. That is, if  $r_C = r_A + r_B$ , then  $R_{AB} = R_C$ . Therefore what was learned about each CS preserved the additivity between their  $r$ s, indicating that the relationship between learning and  $r$  must be linear. In other words, the present findings strongly suggest that  $r$  was in effect the content of the rats' learning, a conclusion that is entirely in keeping with the assertions of rate-based models of conditioning, in particular RET (Gallistel & Gibbon, 2000). This conclusion has a number of implications. One is that the relationship between two CSs and their compound should be symmetrical. That is, when rats are trained with a compound, what they learn should be divided between the two CSs. This could be tested by conditioning a compound XY at a rate of  $r_{XY}$ , while concurrently reinforcing one half of this compound (Y) at a rate  $r_Y$ . In this case, learning about X should equal what is learned when  $r = [r_{XY} - r_Y]$ . We are currently conducting experiments that test this prediction.

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