

**CS-dependent response probability in an  
auditory masked-detection task:  
Considerations based on models of Pavlovian  
conditioning**

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Experimental studies were performed using a Pavlovian-conditioned eyeblink response to measure detection of a variable-sound-level tone (T) in a fixed-sound-level masking noise (N) in rabbits. Results showed an increase in the asymptotic probability of conditioned responses (CRs) to the reinforced TN trials and a decrease in the asymptotic rate of eyeblink responses to the non-reinforced N presentations as a function of the sound level of the T. These observations are consistent with expected behaviour in an auditory masked detection task, but they are not consistent with predictions from a traditional application of the Rescorla–Wagner or Pearce models of associative learning. To implement these models, one typically considers only the actual stimuli and reinforcement on each trial. We found that by considering perceptual interactions and concepts from signal detection theory, these models could predict the CS dependence on the sound level of the T. In these alternative implementations, the animal's response probabilities were used as a guide in making assumptions about the "effective stimuli".

In recent psychophysical studies (Early et al., 2001; Zheng et al., 2001), we used a Pavlovian-conditioned eyeblink in rabbit to study detection of a tone (T) that was presented in compound with a noise masker (N). These experiments used a feature positive procedure, where TN presentations were always accompanied by the unconditioned stimulus (US), and the noise alone, N, was presented frequently and never with the US. These presentation types are designated  $TN^+$  and  $N^-$ , respectively. This training resulted in substantial responding to the TN compound and little responding to N. To measure sensitivity for detecting T in the presence of N,

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the sound level of T (T SPL)<sup>1</sup> was varied using a tracking paradigm (Levitt, 1971) to identify the T SPL that yielded 50% conditioned responding on TN<sup>+</sup> trials. These experiments showed that percentage of conditioned responses (CRs) for TN<sup>+</sup> trials systematically increased with increasing T SPL. Similar observations have been made utilizing different procedures (Kamin, 1965; Martin, Lonsbury-Martin, & Kimm, 1980), and psychometric functions relating percentage of CRs to T SPL have been well documented in the hearing literature (e.g., Fay, 1988).

The change in response probability on TN<sup>+</sup> trials with T SPL in our experiments was accompanied by a low but persistent probability of an eyeblink response to N<sup>-</sup> presentations that varied inversely with T SPL. These “false alarms” are a well-known phenomenon in studies of detection of signals in noise (e.g., Green & Swets, 1974). Although the concept of false alarms is typical in signal detection theory, they are difficult to understand in terms of Pavlovian conditioning models (e.g., Pearce, 1987; Rescorla & Wagner, 1972). One difficulty in interpreting the false alarms is that these models predict that asymptotic associative strength (henceforth designated  $V^\infty$ ) becomes zero after extensive N<sup>-</sup> presentations.

In this report, we examine the extent to which the measured probabilities of conditioned responding can be analysed and interpreted in the context of the Rescorla and Wagner (RW) (1972) and Pearce (1987) models of associative learning. These models are representative of two major views of Pavlovian conditioning: The RW model is an elemental model, whereas the Pearce model is a configural model. However, neither the RW nor the Pearce models predict that asymptotic associative strengths vary with the sound pressure level of the conditioning stimulus (CS). Thus, if a given US results in a high  $V^\infty$  for one sound level of the CS, both models would predict the same  $V^\infty$ , and in all likelihood the same response probability, for any audible CS because  $V^\infty$  is determined by the properties of the US, not the CS. Both models include learning-rate parameters that are commonly associated with strength or salience of the CS, but they have no effect on  $V^\infty$ . Although there is a complex relation between the underlying associative strength that is assumed to accrue to a CS and the proportion of conditioned responding that a CS affords (e.g., Durlach, 1989; Miller & Matzel, 1989), the amount of conditioned responding to a CS after extensive training may reflect the terminal associative strength of a CS (e.g., Hendry, 1982).

To further explore our psychophysical results in the context of these models, we tested the same animals as those that were used in our previous psychophysical experiments (see Early et al., 2001; Zheng et al., 2001). Two animals were tested at several fixed T SPLs (estimated from post hoc analysis of results of the tracking procedure) that resulted in approximately 50%, 70%, and 100% CRs. The results of these experiments confirmed that asymptotic performance varied with T SPL and corresponded to the performance expected on the basis of psychometric functions extracted from the tracking data.

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<sup>1</sup>“T SPL” in this report refers to the sound level in dB SPL of the acoustic stimuli. To avoid confusion with the commonly used phrase “level of responding”, we use this expression rather than “T level”, and we refer to the behavioural responses in terms of the proportion or probability of responding. In addition, we use “CS sound pressure level” rather than the commonly used expression “CS intensity” to avoid erroneously referring to the auditory stimulus in terms of intensity.

## Modelling a masked-detection paradigm with the RW and Pearce models

In this study we seek to explain the observation of these T-SPL-dependent response probabilities in the context of the two Pavlovian-conditioning models. Concepts from signal detection theory were applied to the modified treatment of the trials. By considering the responses of the animal on each trial in addition to the acoustic stimuli delivered and reinforcement present, we explored an alternative description of the trials and their effect on predicted  $V^\infty$ . This approach allowed us to predict our observations within the confines of the RW and Pearce models.

The RW and Pearce models predict associative strength solely on the basis of the stimuli and the reinforcement used in a given experimental design. In our feature-positive case, there were two types of presentation when categorized solely by the stimuli and the reinforcement: (1)  $TN^+$  (tone-plus-noise trials that were always reinforced with the US) and (2)  $N^-$  (noise-alone presentations that were never reinforced).

Under these contingencies, if  $\lambda$  (maximum associative strength for a particular US) had a value of 1 on  $TN^+$  trials in both models and  $N^-$  presentations were never reinforced ( $\lambda = 0$ ), both models predict that the asymptotic associative strength would be 1 for  $TN^+$  trials ( $V_{TN}^\infty = 1$ ) and 0 for  $N^-$  presentations ( $V_N^\infty = 0$ ), regardless of CS sound pressure level. This prediction cannot explain the observed behaviour of T-SPL-dependent response probability. Because  $N^-$  presentations occurred approximately 40 times more often than the  $TN^+$  trials, any initial associative strength gained by  $N^-$  due to its reinforcement when presented with  $T$  was rapidly extinguished. Therefore, according to these models  $T$  should acquire all of the associative strength, whereas the associative strength of  $N^-$  should be minimal. In the RW model,  $N^-$  initially acquires strength as an element of the compound  $TN$  that is being reinforced but loses strength on the  $N^-$  presentations (extinction trials). In the Pearce model,  $N^-$  acquires initial excitatory strength indirectly through similarity to and generalization from the  $TN$  stimulus but loses it because of direct inhibitory strength acquired on the  $N^-$  presentations.

## Treatment of presentations on the basis of signal detection theory

Stated in the language of signal detection theory, the noise-alone ( $N^-$ ) and tone-plus-noise ( $TN^+$ ) are overlapping distributions with different means. Hence, a particular sample chosen from the  $TN^+$  distribution may have a higher probability of belonging to the  $N^-$  distribution and, therefore, may sound more like noise alone than like tone-plus-noise. As the  $T$  SPL is increased the overlap is reduced. Conversely, a sample drawn from the  $N^-$  distribution may sound more like it belongs in the  $TN^+$  distribution. If the responses of the animal are considered when categorizing trials, each of the two trial types described earlier can be subdivided into two subtypes utilizing terminology from signal detection theory. In this classification scheme, a given  $TN^+$  trial is either a “hit” (resulted in a CR) or a “miss” (resulted in no CR); an  $N^-$  presentation is a “correct rejection” (resulted in no CR) or a “false alarm” (resulted in a CR). When  $T$  SPL increases, “misses” and “false alarms” should decrease.

Within the framework of the traditional RW and Pearce models, a trial classified as a “miss” is modelled as  $TN^+$ , a reinforced tone-plus-noise trial.  $TN^+$  trials increase  $V_{TN}$  whether the animal responds or not. However, when two auditory stimuli are used (in this case, a tone and a

noise), the possibility of direct masking and perceptual interaction becomes an issue. Myers, Vogel, Shin, and Wagner (2001) have discussed the influence of perceptual interactions on the results of experiments in negative patterning and summation that appeared contradictory. If one assumes that the tone is completely masked and therefore is inaudible when a “miss” occurs, then the intended  $TN^+$  trial effectively becomes an  $N^+$  trial. The presence of these trials, which we denote as  $(T)N^+$  trials, would have the effect of increasing  $V_N^\infty$  ( $V_N^\infty > 0$ ) instead of  $V_{TN}^\infty$ . We refer to instances of  $(T)N^+$  trials as “misses”; this treatment considers the animal’s failure to respond to the  $TN^+$  stimuli as an indication that the effective stimulus may not have been the intended stimulus. This is a probabilistic event, and the assumption is made only after verification that the animal can achieve 100% CRs for a high CS sound pressure level. The probability of masked tones or “misses” decreases monotonically with increasing T SPL and response probability.

Similarly, in a traditional stimulus-based implementation of the learning models, a “false alarm” is modelled as  $N^-$ , a non-reinforced noise-alone presentation. There are several reasons to believe that the false alarms in our previous studies were actually CRs and not random eyeblinks. First, they occurred consistently at rates higher than the spontaneous eyeblink rate of rabbits (reported as 1–3 per hour, Gormezano, 1966, which is consistent with our own observations); second, the eyeblink trace of “false alarms” had the timing and topography of CRs (see Figure 1, later); and third, the “false alarm” rate was inversely proportional to the T SPL being tested. The traditional model implementations would not be influenced by “false alarms”, and  $N^-$  presentations would not influence the ultimate  $V_{TN}^\infty$ . In the short term,  $N^-$  presentations reduce  $V_{TN}$  as either an element of the compound (in the RW model) or by similarity and generalization (in the Pearce model). However, if one assumes that a “false alarm” occurs because of a response to a sensory percept, as is typically assumed in signal detection theory, an intended  $N^-$  presentation effectively becomes a  $TN^-$  trial. The presence of these trials, which we denote as  $tN^-$  trials, decreases  $V_{TN}^\infty$  ( $V_{TN}^\infty < 1$ ) due to partial reinforcement.

With these alternative descriptions, four types of presentation can be denoted:  $TN^+$  (“hits”),  $(T)N^+$  (“misses”),  $N^-$  (“correct rejections”), and  $tN^-$  (“false alarms”). Given these descriptions, revised implementations of the RW and Pearce models may be considered. Here we investigated how asymptotic associative strengths vary with CS sound pressure level for these revised models.

In the RW model, the asymptotic associative strength can be derived analytically for a particular stimulus or compound that is partially reinforced as follows (Rescorla & Wagner, 1972, p. 85):

$$V = \frac{\pi\beta_1\lambda_1 + (1-\pi)\beta_2\lambda_2}{\pi\beta_1 + (1-\pi)\beta_2} \quad 1$$

where  $\beta_1$  and  $\lambda_1$  are associated with one stimulus,  $\beta_2$  and  $\lambda_2$  are associated with a second stimulus, and  $\pi$  is the proportion of reinforced trials for the stimulus for which  $V$  is being calculated. Following Rescorla and Wagner (1972),<sup>2</sup> when  $\lambda_1 = 1$  and  $\lambda_2 = 0$  and this equation is applied to the current experiment involving TN compounds:

<sup>2</sup>Equations 2 and 3 incorporate the correction of the typographical error in Rescorla and Wagner (1972), as noted by Gibbon (1981).

$$V_{TN}^{\infty} = \frac{\pi_{TN}\beta_{TN}}{\pi_{TN}\beta_{TN} + (1 - \pi_{TN})\beta_N} \quad 2$$

and N presentations:

$$V_{TN}^{\infty} = \frac{\pi_N\beta_{TN2}}{\pi_N\beta_{TN} + (1 - \pi_N)\beta_N} \quad 3$$

where  $\pi$  is calculated as follows:

$$\pi_{TN} = \frac{n_1 - n_{(T)}}{n_T - n_{(T)} + n_i} \quad 4$$

and

$$\pi_N = \frac{n_{(T)}}{n_N + n_{(T)} - n_i} \quad 5$$

where  $n_T$  is the number of tone trials,  $n_N$  is the number of noise trials,  $n_{(T)}$  is the total number of “misses” [(T)N<sup>+</sup> trials], and  $n_i$  is the number of “false alarms” (tN<sup>-</sup> trials). These above expressions were the basis for the computation of the RW model predictions presented later. Note that to simulate our paradigm,  $n_N$  was set equal to ( $n_T * 40$ ). The value of the rate parameter for the reinforced presentations,  $\beta_{TN}$ , was set to twice the value of that for non-reinforced presentations,  $\beta_N$ .<sup>3</sup> To implement the traditional RW and Pearce models, the values of each parameter in equations 2 through 5 were

$$n_{(T)} = 0; n_i = 0; \therefore \pi_{TN} = 1 \text{ and } \pi_N = 0$$

whereas for the revised model, the parameters values were

$$0 < n_{(T)} < 1; 0 < n_i < 1; \therefore 0 < \pi_{TN} < 1 \text{ and } 0 < \pi_N < 1$$

The values of  $n_{(T)}$  and  $n_i$  are set to 0 in the traditional stimulus-based approach to classifying the presentations. In the revised implementation of the model, where  $n_{(T)}$  or  $n_i$  are non-zero, the animal’s responses are considered to be due to perceptual interactions; therefore, “misses” and “false alarms” affect the results. The values of  $n_{(T)}$  and  $n_i$  used in these calculations were derived directly from our experimental data. It is clear from the values of  $\pi$  for each case that the predicted values of  $V^{\infty}$  for the traditional models are  $V_{TN}^{\infty} = 1$  and  $V_N^{\infty} = 0$ , whereas the predicted values for the revised model are  $0 < V_{TN}^{\infty} < 1$  and  $0 < V_N^{\infty} < 1$ .

The goal of this study was to explain the observation of these T-SPL-dependent response probabilities in the context of the two Pavlovian-conditioning models. Concepts from signal detection theory were applied to the modified treatment of the trials. By considering the responses of the animal on each trial in addition to the acoustic stimuli delivered and reinforcement present, we explored an alternative description of the trials and their effect on predicted  $V^{\infty}$ . This approach allowed us to predict our observations within the confines of the RW and Pearce models. Whereas previous studies have characterized the results of discrimination procedures in terms of signal detection theory (Kehoe, Horne, & Horne, 1993; Suboski, 1967), this study represents an attempt to understand the way in which the Pavlovian conditioning

<sup>3</sup>In our calculations,  $\beta_{TN}$  (associated with the US) was set to .1 and  $\beta_N$  (associated with the absence of the US) was set to .05. In Equations 2 and 3, it is the ratio of  $\beta_1$  to  $\beta_2$  that is important; in fact, if  $\beta_1 = \beta_2$ , then the equations simply reduce to  $V^{\infty} = \pi$ . That is, the asymptotic associative strength will be equal to the proportion of reinforcement.

contingencies may influence the psychophysical estimates obtained in the auditory masked-detection experiments.

## EXPERIMENT

### Method

#### *Masked-detection paradigm in rabbit*

Two Dutch-belted rabbits (2.0–2.5 kg), R4 and R7, were subjects in the behavioural experiments. General methods for the study of Pavlovian conditioning in the rabbit were developed by Gormezano (1966). The methods we have used for the generation and delivery of acoustic stimuli, rabbit care and training, and Pavlovian conditioning of the eyeblink response have been described in detail previously (Early et al., 2001; Zheng et al., 2001). Briefly, acoustic stimuli were generated, attenuated, and mixed using a programmable TDT system (Tucker Davis Technologies, Gainesville, Florida). Calibrated acoustic stimuli were presented to the rabbit through earphones (Beyerdynamic DT 48; Beyerdynamic, Heilbronn, Germany), which were coupled to custom-made soft plastic earmoulds (Perform H/H; Hal Hen, Long Island City, New York).

#### *Pavlovian-conditioning experiments*

The CS was a 500-ms, 500-Hz tone. The US was a 100-ms, 0.9-mA electrical shock presented to electrodes, either two silver-chloride electrodes (R4; TD-23; Med Associates, St. Albans, VT, USA) or two wound clips positioned posterior to the left orbit (R7). The US was always paired with the CS and occurred during the last 100 ms of the CS. The CS-US combination was presented approximately once per minute. The intertrial interval varied randomly between 49.5 and 70.5 s. Gaussian noises of 500 ms and spectrum level of 40 dB (equivalent to a root-mean-square, or rms, level of 75 dB SPL), with 2900-Hz bandwidth (100 Hz to 3000 Hz), were used as maskers. A noise masker was presented simultaneously with every CS presentation. Gaussian noises of 500-ms duration were also presented alone once every 1.5 s between CS presentations, for a total of 33 to 47  $N^-$  presentations between every  $TN^+$  trial. Identical stimuli were always presented to both ears.

Eyeblink responses were detected with a photodiode-phototransistor pair that was aimed at the rabbit's eyelid. The signal from the photodiode was low-pass filtered (cutoff frequency of 60 Hz), sampled at a frequency of 1 kHz, and smoothed with a 5-point average. The onset of the eye blink response was determined to occur when the derivative of the eyeblink position signal exceeded a threshold criterion. This criterion was initially adjusted in an effort to achieve sensitive detection of eyeblinks, as our goal was to measure sensitivity of the animals to T. Eyeblinks with amplitudes of at least 0.1–0.2 mm within the required time window were detected by the criterion value used in these experiments. A response was considered a CR if it began during the CS and before the onset of the US. Any response that began after the onset of the US was counted as an unconditioned response (UR). Eyeblink responses that occurred during  $N^-$  presentations were also recorded.

Both rabbits were tested in previous experiments, and their training and acquisition of the Pavlovian-conditioned eyeblink response has been described previously (Early et al., 2001; Zheng et al., 2001). All responses were obtained using the same conditioning technique and US. Briefly, both animals were trained to respond to 500-ms tones in the presence of simultaneous noises ( $TN^+$  trials). In previous experiments over several months, the animals were tested for detection of the tone using a standard tracking procedure (Early et al., 2001; Zheng et al., 2001). In this procedure, the T SPL for each trial was based on the animal's response in previous trials.

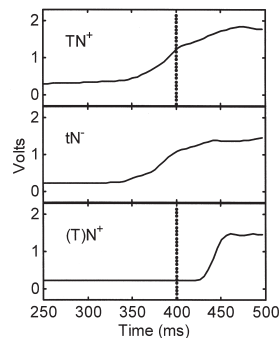
Two different tracking algorithms were used: In one case, the T SPL was based on the previous  $TN^+$  trial. If the previous  $TN^+$  trial resulted in a CR, the T SPL for the subsequent  $TN^+$  trial was reduced by 2 dB; if the previous  $TN^+$  trial did not result in a CR, the T SPL was increased by 2 dB on the subsequent  $TN^+$  trial. This procedure is referred to as a one-up, one-down procedure. The average of the T SPLs where the sequence reverses directions is an estimate of the T SPL where the animal responds with a CR on 50% of the  $TN^+$  trials (Levitt, 1971).

In the second tracking algorithm, the T SPL was reduced by 2 dB only after two sequential  $TN^+$  trials that both resulted in CRs, and the T SPL was increased by 2 dB after a single  $TN^+$  trial that did not result in a CR. If a  $TN^+$  trial resulted in a CR but the previous  $TN^+$  trial had not resulted in a CR the T SPL remained unchanged for the subsequent  $TN^+$  trial. The average of the T SPLs at the reversals for this two-down, one-up procedure provides an estimate for the T SPL at which the animal responds with CRs on approximately 70% of the  $TN^+$  trials (Levitt, 1971). Based on the tracking data, T SPLs corresponding to approximately 50%, 70%, and 100% performance were chosen for fixed-T-SPL testing. Each of these T SPLs was tested for 5 to 24 sessions per condition.<sup>4</sup> Each session consisted of approximately 3280 stimulus presentations containing 80  $TN^+$  trials and 3200  $N^-$  presentations. Each session lasted approximately 2 hours, and one session was run per day for each animal.

## Results

Figure 1 shows three recorded eyeblink responses from one animal in one session: a CR plus a UR recorded on a  $TN^+$  trial (top panel), a CR recorded on an  $N^-$  presentation ( $tN^-$  or “false alarm”—middle panel), and a UR recorded on a  $TN^+$  trial [( $T$ ) $N^+$  or “miss”—bottom panel].

The animal's response never affected the CS-US contingencies: The US was delivered on every  $TN$  presentation and was never delivered on an  $N$  presentation. Therefore the presented, intended stimulus configuration consisted only of  $TN^+$  and  $N^-$  types. The response probabilities described earlier are simply alternative descriptions of the “effective” stimuli and trial types that were used in the revised implementation of the models.

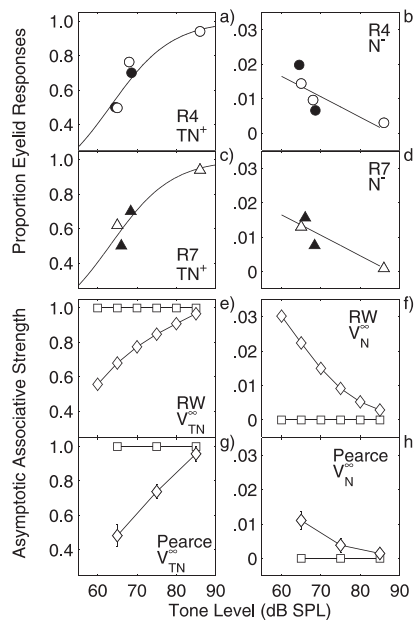


**Figure 1.** Eyeblink traces recorded from the photodiode/phototransistor pair in volts, corresponding to a “hit” (top), a “false alarm” (middle), and a “miss” (bottom). The dotted line indicates the onset of the 100-ms, 0.9-mA shock 400 ms after the onset of the  $TN^+$  trials at 0. The first 250 ms of the eyeblink traces are omitted for clarity. Eyeblinks shown are three consecutive eyeblinks from Session 207 of rabbit R7 (top is stimulus presentation #958, middle is #949, and bottom is #991).

<sup>4</sup>For most fixed-T-SPL conditions, approximately 20 sessions were completed to ascertain that asymptotic performance had been obtained and the percentage of CRs was stable across several sessions. For high T SPLs, at which the animal's response to  $TN^+$  trials was approximately 100%, fewer sessions were completed.

In Figure 2, the proportions of eyeblink responses on  $TN^+$  trials and on  $N^-$  presentations are shown for each animal. Response probability varied with stimulus SPL for both  $TN^+$  trials (panels a and c) and  $N^-$  presentations (panels b and d). The plots in panels a and c depict the proportion of “hits” as a function of T SPL. For both animals, the probability of a “hit” increased with increasing T SPL. Conversely, the probability of a “false alarm” decreased with increasing T SPL (panels b and d). Both of these results would be expected for an auditory-detection task of this type. It is plausible and intuitive to suppose that false alarms should be more frequent at low T SPLs; in contrast, when testing with high T SPLs, responses to  $N^-$  presentations would not be expected.

In the RW model, the  $TN$  compound consists of the elements T, the tone, and N the noise, N. The associative strength of  $TN$  is the simple sum of the associative strengths of T and N ( $V_{TN} = V_T + V_N$ ). In the Pearce model, the  $TN$  stimulus is a unique configuration but has similarity, and hence generalizes, to both T and N. The parameters and equations used to generate the results for each model are given in the Appendix. As mentioned previously, some model



**Figure 2.** Experimental observations from tracking and fixed-T-SPL sessions (panels a–d) and model predictions (panels e–h). Panels a, c: Probability of CRs on  $TN^+$  trials (“hits”) as a function of T SPL for two animals (R4, a; R7, c). Panels b, d: Probability of CRs on  $N^-$  trials (“false alarms”) as a function of T SPL (R4, b; R7, d). The T SPLs that resulted in 50%- and 70%-conditioned responding on the tracking procedures are represented by closed symbols. The proportions of responses at each fixed T SPL are represented by open symbols. Panel e: Predicted  $V_{TN}^{\infty}$  for the RW model. Panel f: Predicted  $V_N^{\infty}$  for the RW model. The square symbols in each panel represent the results for the traditional model, and the diamonds represent the revised model. For each case, the predicted  $V^{\infty}$  is given for six stimulus sound levels: 60–85 dB SPL in 5-dB steps. Panel g: Mean predicted  $V_{TN}^{\infty}$  for the Pearce model. Panel h: Mean predicted  $V_N^{\infty}$  for the Pearce model. Error bars indicate standard deviations based on 10 repetitions of the simulations. The square symbols in each panel represent the results for the traditional model, and the diamonds represent the revised model. For each case, the predicted  $V^{\infty}$  is given for simulations at three stimulus sound levels: 65–85 dB SPL in 10 dB steps.



parameters were estimated directly from the experimental data. The proportion of “misses” (1 – proportion of “hits”; panels a and c) was used to determine the average number of “misses,”  $n_{(T)}$ , that would have occurred at a given T SPL. Linear interpolation was used to determine the value of the model parameter  $n_t$ , the number of “false alarms,” that would have occurred in a session with a given T SPL (see panels b and d).

The models were studied with the previous analytical descriptions for the RW model and with trial-by-trial simulations for both the RW and Pearce models. To our knowledge, the equations for the asymptotic associative strengths in the Pearce model have yet to be developed. In the simulations of both models, the random occurrence of “misses” and “false alarms” caused expected fluctuations in the associative strengths over time that resulted in slightly different asymptotic values each time the simulation was run. Means and standard deviations for 10 repetitions of the simulation results for the Pearce model are presented in Figure 2. For the RW model, the results presented were based on the analytical asymptotic values, using the equations presented previously, and hence have no variance.

Model predictions of  $V^\infty$  are shown in Figure 2 for both the traditional and revised versions of the RW model (panels e and f) and the Pearce model (panels g and h).  $V_{TN}^\infty$  and  $V_N^\infty$  showed the same trends for both the RW and Pearce models. Each panel shows the values of  $V^\infty$  for TN ( $V_{TN}^\infty$ ) (panels e and g) or N ( $V_N^\infty$ ) (panels f and h). The predictions for the traditional implementation of the models (squares) are all independent of T SPL, as expected, with  $V_{TN}^\infty$  equal to 1 and  $V_N^\infty$  equal to 0. The revised implementation of the model that includes both “misses” and “false alarms” (diamonds) predicts increasing  $V_{TN}^\infty$  with T SPL (panels e and g) and decreasing  $V_N^\infty$  with T SPL (panels f and h) for both the RW and the Pearce models. The trends in the responses of the revised models for both  $V_{TN}^\infty$  (Figure 2, panels e and g) and  $V_N^\infty$  (panels f and h) are consistent with the T-SPL-dependent proportions of eyeblink responses that were observed in the behavioural experiments (panels a and c, and panels b and d, respectively).

## Discussion

This study began with a set of conditioned responses to tones that were systematically varied in sound pressure level in order to determine the animal’s sensitivity for detection of tones in a masking noise (Early et al., 2001). The trends in the results were not surprising given the results of basic studies of auditory behaviour; for example, the asymptotic probability of “hits” increased with increased T SPL, whereas the “false alarms” decreased. However, this straightforward result would not be anticipated on the basis of a traditional implementation of the RW or Pearce models of Pavlovian conditioning. In the standard implementation of those models, the US determines asymptotic performance, not the salience of the CS (e.g., Miller, Barnet, & Grahame, 1995). Although near-100% CRs were consistently obtained in the present study when the T SPL was high, much lower response probabilities were obtained when the T SPL was lowered, even though the US had not changed.

Miller et al. (1995) have noted that a limitation of the RW model is its inability to account for  $V^\infty$ , and by inference the probability of a response (e.g., Frey & Sears, 1978), being dependent on the CS sound pressure level, as is the case in hearing and in other sensory systems. One way to explain this performance within the context of the RW model is to vary the maximum associative strength,  $\lambda$ , with the sound pressure level of the CS (e.g., Damianopoulos, 1987). However, this change would add complexity to the RW model and could undermine its

generality (Miller et al., 1995, see Failure No. 10, p. 374). When examining this behavioural result with the Pearce model, an obvious consideration is the similarity factor,  $S$ , which determines the amounts of generalized learning. Pearce notes (1987, p. 66) in an example using a tone (T) and a light (L) that “the relative intensities of T and L will exert a profound influence on the values of  $S$ ”. Although changes in  $S$  do affect excitatory and inhibitory strengths, they do not affect the ultimate associative strengths or values of  $V^\infty$  in this case. Therefore, neither model can currently account for changes in the probability of responding to  $TN^+$  or  $N^-$  presentations as a function of T SPL (or CS sound pressure level).

To determine whether the adaptive tracking trends would be observed with tones presented at fixed T SPLs, the initial experimental results were extended in the results presented here. Indeed, as shown in Figure 2 (panels a and c), the asymptotic performance for several fixed T SPLs was consistent with results from adaptive tracks. The probability of CRs was clearly dependent on T SPL with a fixed US that was sufficient to elicit 100% responding at high T SPLs.

As illustrated in Figure 2 (panels e–h; squares), traditional implementations of the models, in which associative strength is affected only by the stimulus properties and reinforcement, could not explain the observed results. When perceptual interactions, and therefore “effective stimuli” that differed from the intended stimuli were considered, the model predictions were similar to the observed trends (Figure 2, panels e–h, diamonds). In the traditional models, all  $TN^+$  trials are treated in the same way, regardless of the animal’s response. Our modified implementations treated  $TN^+$  trials as either “hits” or “misses” on the basis of the animal’s response and the assumption that the tone is essentially inaudible on some trials with low T SPLs (i.e., it sounds more like noise alone). The response probabilities yield an estimate of the proportion of trials on which this perceptual interaction may be occurring. In addition,  $N^-$  presentations were treated as either “correct rejections” or “false alarms”, again on the basis of both the animal’s response and the assumption that some noise samples sound as though they have weak tones embedded in them. Inclusion of these four response types (“hits”, “misses”, “correct rejections”, and “false alarms”) yielded T SPL dependence of both  $V_{TN}^\infty$  and  $V_N^\infty$ , which was consistent with observed trends in behaviour. This interpretation of presentation types is based on signal detection theory, assuming overlap between the distributions of N and TN (Green & Swets, 1974).

Our treatment of the four response types is not intended to be exhaustive. For example, the absence of a CR is not necessarily due to an undetected CS, and not every CR to a non-reinforced stimulus presentation is due to a CS-like percept. Furthermore, the signal detection theory approach must be applied with caution because the reflexive nature of the Pavlovian CR precludes the concept of voluntary criterion placement.

An additional limitation (e.g., Miller & Matzel, 1987) of this approach is that we considered the asymptotic performance at each T SPL independently, without considering the history of accrued associative strength due to previous training and testing at other T SPLs. We intentionally tested for long periods of time at each T SPL, until performance was stable over several sessions, to reduce the influence on performance of the T SPL used in initial training and the sequence of T SPLs used in subsequent training and testing. In addition, the testing order of T SPLs differed between animals. Future experiments could systematically explore the interactions between the accrued associative strength due to training at one T SPL followed by testing at another. Our interest in this study was understanding the influence of T SPL on

steady-state performance over an extended period of time; thus we focused on asymptotic performance and models for asymptotic associative strength rather than acquisition.

These results illustrate the potential importance of perceptual interactions and the animal's response in determining the appropriate treatment of stimulus presentations in a conditioning paradigm. In experiments with supra-threshold sensory stimuli that do not mask each other or interact in this way, the effect would not be important. Such stimuli presumably have underlying distributions with very little, if any, overlap. It was the attempt to determine the lowest T SPLs that could be detected in the presence of a masker N that introduced these initially conflicting trends in our observations.

These models provide a quantitative context in which the relative influence of the conditioning paradigm and the underlying auditory sensitivity may be evaluated. This leads to several testable hypotheses. The revised implementation of the models predict that the proportion of CRs at a given tone SPL would increase if the effective stimuli were taken into account, not only in the treatment of stimulus presentations in the analysis, but also in determining which presentations to reinforce. If "false alarms" were reinforced (assuming that the animal is responding to a percept of T during these stimulus presentations),  $V_{TN}^{\infty}$  should increase due to the increased reinforcement of TN. Thus, reinforcing "false alarms" should lead to a higher  $V_{TN}^{\infty}$  for a given T SPL, which in turn should result in a higher proportion of CRs at that stimulus SPL. In addition, the omission of reinforcement on TN trials that are "missed" (assuming that T is inaudible on these trials) should lead to a weaker associative strength between N and the US and presumably to a lower probability of responses to noise alone (i.e., "false alarms") at that stimulus SPL. However, as "false alarms" may also be due to the sensory percept of a tone, they would still be expected to occur even in the absence of reinforcement of "misses". In addition, because "misses" may be due to the lack of a sensory percept of a tone, they would still be expected to occur at low T SPLs even when "false alarms" are reinforced.

These predictions are an example of the influence of the conditioning paradigm on the observed behaviour, which cannot be interpreted simply in terms of sensory ability. In a conditioning paradigm in which the reinforced presentation is not always well above "threshold" (i.e., 100% detectable), the possibility of reinforcement of the background or second stimulus of a compound must be considered. Likewise, whenever a sensory event may give rise to a signal-like sensation on a non-signal presentation, the possibility of non-reinforcement of the intended reinforced stimulus must also be considered.

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## APPENDIX

All simulations were run for 26,240 trials, of which one in 40 was a TN trial, and the rest were N presentations. This number of presentations corresponds closely to eight experimental sessions, each consisting of 80 TN trials and approximately 3200 N presentations, which was a typical size for many of our data sets (e.g., Zheng et al., 2001). The parameters and equations used in simulations of each model are as follows:

RW: All associative strengths were initially set to 0. On  $TN^+$  trial  $i$ ;  
 $\lambda = 1$ ;  $\alpha_T = .5$ ;  $\alpha_N = .5$ ;  $\pi_{TN} = .1$   
 $\Delta V_T(i) = \alpha_T \beta_{TN} [\lambda - V_{TN}(i-1)]$ ;  $\Delta V_N(i) = \alpha_N \beta_{TN} [\lambda - V_{TN}(i-1)]$   
 $V_T(i) = \Delta V_T(i) + V_T(i-1)$ ;  $V_N(i) = \Delta V_N(i) + V_N(i-1)$   
 $V_{TN}(i) = V_T(i) + V_N(i)$

On  $N^-$  presentation  $i$ ;

$\lambda = 0$ ;  $\alpha_N = .5$ ;  $\beta_N = .05$   
 $\Delta V_N(i) = \alpha_N \beta_N [\lambda - V_N(i-1)]$   
 $V_N(i) = \Delta V_N(i) + V_N(i-1)$

Pearce: All associative strengths were initially set to 0. On  $TN^+$  trial  $i$ :

$\lambda = 1$ ;  $\beta_{TN} = .25$ ;  ${}_N S_{TN} = .5$   
 $\Delta E_{TN}(i) = \beta_{TN} [\lambda - V_{TN}(i-1)]$   
 If  $\Delta E_{TN}(i) < 0$  then  $\Delta I_{TN}(i) = |\Delta E_{TN}(i)|$  and  $\Delta E_{TN}(i) = 0$   
 $E_{TN}(i) = \Delta E_{TN}(i) + E_{TN}(i-1)$ ;  $I_{TN}(i) = \Delta I_{TN}(i) + I_{TN}(i-1)$   
 $e_{TN}(i) = {}_N S_{TN} \times E_{TN}(i)$ ;  $i_{TN}(i) = {}_N S_{TN} \times I_{TN}(i)$   
 $V_{TN}(i) = E_{TN}(i) + e_{TN}(i) - [I_{TN}(i) + i_{TN}(i)]$

On  $N^-$  presentation  $i$ ;

$\lambda = 0$ ;  $\beta_N = .25$ ;  ${}_N S_{TN} = .5$   
 $\Delta E_N(i) = \beta_N [\lambda - V_N(i-1)]$   
 If  $\Delta E_N(i) < 0$  then  $\Delta I_N(i) = |\Delta E_N(i)|$  and  $\Delta E_N(i) = 0$   
 $E_N(i) = \Delta E_N(i) + E_N(i-1)$ ;  $I_N(i) = \Delta I_N(i) + I_N(i-1)$   
 $e_N(i) = {}_N S_{TN} \times E_{TN}(i)$ ;  $i_N(i) = {}_N S_{TN} \times I_{TN}(i)$   
 $V_N(i) = E_N(i) + e_N(i) - [I_N(i) + i_N(i)]$