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The acquisition of conditioned responding

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Abstract

This report analyzes the acquisition of conditioned responses in rats trained in a magazine approach paradigm. Following the suggestion by Gallistel, Fairhurst and Balsam (2004), Weibull functions were fitted to the trial-by-trial response rates of individual rats. These showed that the emergence of responding was often delayed, after which the response rate would increase relatively gradually across trials. The fit of the Weibull function to the behavioral data of each rat was equaled by that of a cumulative exponential function incorporating a response threshold. Thus the growth in conditioning strength on each trial can be modeled by the derivative of the exponential – a difference term of the form used in many models of associative learning (e.g., Rescorla & Wagner, 1972). Further analyses, comparing the acquisition of responding to a continuously reinforced stimulus (CRf) and a partially reinforced stimulus (PRf), provided further evidence in support of the difference term. In conclusion, the results are consistent with conventional models that describe learning as the growth of associative strength, incremented on each trial by an error-correction process.

Key words: Pavlovian conditioning; Rat; Magazine approach; Learning curve; Partial reinforcement

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Traditionally, models of conditioning have treated learning as the gradual accumulation of conditioning strength (e.g., Hull, 1943). One of the earliest computationally-refined proposals describes learning as trial-by-trial increments in associative strength (V), with each increment being directly proportional to the difference between the maximum strength supported by the events that comprise each conditioning episode and the strength already acquired across each conditioning trial up to and including the previous one (Bush & Mosteller, 1951). Conceptually, this rule equates learning with an "error correction" process that minimizes the difference between the observed relations between events and stored associative information pertaining to those events. A simple formalization of this operation is presented in Equation 1.

$$\Delta V_t = k \cdot (\lambda - V_{t-1}) \qquad (1)$$

Here V_t is the associative strength of the conditioned stimulus (CS) after trial t, λ is the maximum associative strength supported by the unconditioned stimulus (US), and k is a rate parameter. This equation is at the heart of more recent models of associative learning, the best known of these being the Rescorla-Wagner (1972) model. But its general form, that ties learning to an error term, is used in many other models of associative learning (e.g., Mackintosh, 1975; Pearce, 1994; Pearce & Hall, 1980; Sutton & Barto, 1981; Wagner, 1981) and even in connectionist models of human cognition (e.g., Gluck & Bower, 1988; McClelland & Rumelhart, 1985; Rogers, 2004). The integral of Equation 1, $\lambda \cdot (1\text{-}e^{-k \cdot t})$, is the cumulative distribution of an exponential function with asymptote equal to λ and slope determined by k. This exponential function describes the predicted "learning curve".

While the above description of learning has proved highly successful in accounting for many empirical features of conditioning, it has been less successful in describing the form of the acquisition function itself. In many conditioning preparations, the emergence or increase in conditioned responding across trials is sigmoid, in that responding initially remains low for some number of trials before it increases towards an asymptote (Mackintosh, 1974; Spence, 1956). This stands in contrast to the exponential learning curve in which the largest increment in conditioning occurs on trial 1, and the rate of learning slows thereafter. The sigmoid shape of many learning curves has long been interpreted as evidence of a performance threshold affecting the response output of the organism (Hull, 1943; Mackintosh, 1974; Spence, 1956). Thus, the early growth of conditioning strength does not produce observable changes in behavior as long as the cumulative conditioning strength remains below that required for the organism to respond. As presented in Equation 2, we can formalize this by defining response strength, R, on trial t as equal to the integral of Equation 1 minus a threshold, θ, with the qualification that R_t cannot be less than zero.

$$\text{If } \left[\lambda \cdot \left(1 - e^{-k \cdot t}\right)\right] < \theta, \; R_t = 0,$$

$$\text{else } R_t = \lambda \cdot \left(1 - e^{-k \cdot t}\right) - \theta \qquad (2)$$

The incremental view of learning has recently come under renewed attack by Gallistel, Fairhurst and Balsam (2004). These authors favor models of learning that attribute conditioned responding to a decision process in which the organism begins to respond when accumulated evidence about the timing or probability of the US exceeds a decision threshold (e.g., Gallistel & Gibbon, 2000). According to these models, the appearance of responding across training should resemble a step function – the organism does not respond for some number of trials then suddenly begins to respond at full asymptotic strength once the evidence for the occurrence of the US exceeds the decision threshold. Gallistel et al. (2004) argue that evidence for a gradual increase in conditioned responding across training is an artifact of data averaging across multiple subjects in an experiment. They point out that

the emergence of responding in individual subjects may in fact be very abrupt but this abrupt change in responding is "smoothed" into a gradual acquisition curve when data from individual subjects are averaged. Such smoothing would occur as long as there are differences between subjects in the time at which they show an abrupt change in responding. Indeed, if the probability of each subject reaching its decision threshold were uniform over time, averaging across such step functions would produce a cumulative exponential distribution equivalent to the conventional error-driven learning curve. Thus Gallistel et al. (2004) rightly argue that the "true" shape of the learning curve can only be ascertained by examining acquisition of conditioned responding in individual subjects. When analyzed in this way, Gallistel et al's own survey of experimental data revealed that, in a variety of conditioning paradigms, the acquisition of conditioned responses was more abrupt than might be expected based on an incremental learning process. However, this conclusion has been challenged recently (Kehoe, Ludvig, Dudeney, Neufeld, & Sutton, 2008). In a fine-grained analysis of nictitating membrane responses in individual rabbits across the course of conditioning, Kehoe et al. observed that the magnitude of the response increased in a continuous manner across training.

In this paper we present detailed analyses of data from two experiments that study the acquisition of conditioned responding in rats using the magazine approach paradigm. This paradigm measures explicit goal-tracking behavior (entries into the food magazine), which should represent a relatively unambiguous index of learned anticipation of the US. We have recently shown that group-averaged acquisition functions in this paradigm conform very closely to a simple exponential function (Thein, Westbrook, & Harris, 2008), though as noted above, this could be consistent with either an incremental learning process or arise as an artifact from averaging over many individual step-functions. In both experiments presented here, rats were trained with discrete CSs that were followed by delivery of a food pellet. Magazine activity was recorded during CS presentation on every trial. Tracking the emergence of conditioned responding across single trials in individual rats is very difficult due to the high degree of variability in response rate from one trial to the next. To solve this problem, rather than averaging data across many trials (which may miss an abrupt change in response rate) or across subjects, we have followed the suggestion by Gallistel et al. (2004) to fit the cumulative distribution of a Weibull function to the data record for each individual rat. This three-parameter function, presented in Equation 3, is used to describe the central tendency of each rat's behavior on each trial across the course of the experiment.

$$R_t = \lambda \cdot \left(1 - e^{-(t/\beta)^s}\right) \qquad (3)$$

The Weibull function is particularly useful for the present purpose because it is relatively neutral about the ultimate shape of the acquisition function. When s = 1, Equation 3 is identical to the integral of Equation 1 (with $\beta = 1/k$). For values of $s > 1$, Equation 3 describes a sigmoid function with slope proportional to s (when $s >> 1$, Equation 3 approaches a step function). Thus the Weibull function provides relatively objective information about the shape of the acquisition function in that it can describe a step function or an incremental learning curve.

The principal objective of this study was to test whether the emergence of conditioned responding is adequately described as a gradual incremental process, as implied by models of learning that use a difference term to compute associative change, or whether responding appears abruptly. This objective was approached in two ways. First, Weibull functions were fitted to the behavioral data of individual rats, and these functions were used to estimate how abruptly or gradually responding increased for each rat. Second,

Equations 2 and 3 were compared in their ability to provide an adequate fit to the behavioral data. If the acquisition of conditioned responding in individual subjects does not follow an incremental learning process, we should expect that Equation 2 will not provide as good a fit to the data as the Weibull function. Behavioral data in which there is a sharp rise in responding after a delay will be particularly difficult for the incremental learning process to describe, since such acquisition curves can only be approximated by Equation 2 if the behavioral threshold is set close to the response asymptote so that responding saturates soon after it appears (Gallistel, et al., 2004). By contrast, the Weibull function (Equation 3) can readily describe such an acquisition curve because the slope of its sigmoid function can vary independently of the latency. Thus, by comparing Equations 2 and 3 in their ability to capture the trend in response rates for each rat across the course of conditioning, the analysis tests the extent to which the acquisition function of individual subjects is adequately described as the incremental process reflected in models of learning that use a difference term to compute associative change. It also provides the opportunity to evaluate those models by revealing the means by which their computational operations can approximate the acquisition of responding (for example, by relying on a high behavioral threshold).

Experiment 1

Experiment 1 trained rats with a single CS for 18 days (a total of 360 trials). The analysis focused on comparing Equations 2 and 3 in their fit to the elevation score (number of responses during the CS minus the number of responses during the preceding interval) on each trial for each rat. The two equations are equivalent when $\theta = 0$ and $s = 1$. Therefore, any difference in the quality of fit of each function to the acquisition data will reveal differences in how well those two parameters capture the shape of the acquisition function. For example, if Equation 3 is consistently better than Equation 2 in fitting the data, this would indicate that the exponential function with response threshold provides the less accurate description of the acquisition process, and thus constitute evidence against the incremental description of learning captured in models based on a difference term. The present analysis also followed the proposal made by Gallistel et al. (2004) to identify a putative "change point" in the response record of each rat. This point refers to the trial on which there was the most abrupt change in the rat's response rate, as would arguably reflect the moment at which the rat's evidence about the occurrence of the US exceeded a decision threshold. Morris and Bouton (2006) applied this analysis to conditioning data collected in the same paradigm used here. When they aligned the response records of all rats according to their individually identified change points, the average response rate, calculated across rats, showed a very abrupt jump on the trial immediately after the change point. Evidence of such an abrupt change is not easily reconciled with the incremental process espoused by conventional learning models. Accordingly, the same analysis has been applied to the data of the present experiment.

Methods

Subjects

Twenty three experimentally naive male Hooded Wistar rats (Rattus norvegicus; weighing 170-240g at the start of the experiment) were bred and housed in the animal colony maintained by the School of Psychology at the University of Sydney. They were housed in groups of 7 or 8 in large white plastic tubs, measuring 26 x 59 x 37cm (height x length x depth), with unrestricted access to water. Three days prior to commencement of the experiment, their access to food was restricted to 2 hr per day (from 6pm-8pm).

Apparatus

Rats were trained and tested in 16 Med Associates™ conditioning chambers measuring 28.5 x 30 x 25 cm (height x length x depth). The end walls of each chamber were made of aluminum; the sidewalls and ceiling were Plexiglas™. The floor of the chamber consisted of stainless-steel rods, 0.5 cm in diameter, spaced 1.5 cm apart. Each chamber had a recessed food magazine in the center of one end wall. A small metal cup measuring 3.5 cm in diameter and 0.5 cm deep was fixed on the floor of each food magazine. Attached to the food magazine was a dispenser delivering 45 mg food pellets (Noyes Formula P; Research Diets Inc, New Brunswick, NJ). Each chamber was enclosed in a sound- and light-resistant wooden shell. Throughout all sessions, fans located in the rear wall provided ventilation; the operation of these created a background level of noise measuring 70dB. Experimental events were controlled and recorded automatically by computers and relays located in the same room. Stimuli could be presented from four spatially separated sources. White noise (78dB) was presented from a speaker mounted on the wall of each 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 chamber. A flashing light (2 Hz; 3.0cd/m^2) was emitted by a 3x5 array of white LEDs, located on the floor of the sound-attenuating shell in front of the chamber. A steady light (30cd/m^2) was produced by an incandescent bulb mounted high on the back wall of the sound-attenuating shell. Only one stimulus was presented to a given rat, and the selection of this CS was counterbalanced across rats.

Procedure

On the day before training began, the rats received a single 20 min magazine training session during which 20 food pellets were presented on a VT 1-min schedule, with no stimulus presentations. The rats then received 18 days of simple conditioning with one stimulus. On each day, the rats were placed into the conditioning chambers for 100 min. During each session, the same stimulus was presented 20 times, for 30 s each time. The interval between stimulus presentations varied randomly, with an average 270 s (and minimum of 50 s). At the termination of every stimulus presentation, a food pellet was delivered into the magazine. Across all 18 days the number of photo-beam interruptions by head entry into the magazine was recorded during each 30-s stimulus and during the 30-s pre-stimulus interval. All procedures were approved by the Animal Care and Ethics Committee at the University of Sydney.

Results

The left panel of Figure 1 shows the average number of responses made during CS presentations on each of the 18 conditioning days. Responding increased steadily over the first 12 days of conditioning, before reaching a plateau of about 17 responses per 30-s stimulus. This averaged acquisition function is very similar to that we reported previously (Thein, et al., 2008); as in that case the averaged elevation scores are very accurately described by an exponential function (R^2 = 0.99).

Analysis of Individual Acquisition Curves

The acquisition functions were estimated for each individual rat. The analysis was abandoned for one rat (#12) because it all but stopped responding after 10 days of training, having previously acquired a modest level of responding to the CS (6 responses above pre-CS baseline). For the remaining 22 rats, we calculated an elevation score on each trial by subtracting the response count in the pre-CS period from the raw response count during the CS presentation. We then found the best-fitting Weibull function for these trial-by-trial elevation scores for each individual rat. Two examples of behavioral data and best-fitting Weibull functions are shown in Figure 2. These examples were chosen because acquisition of

responding in one of these rats (#21) is typical of many rats in this experiment, while the data from the other rat (#2) is unusual in showing a considerable delay in the emergence of responding. The average goodness-of-fit (R^2) for all 22 Weibull functions is 0.303, and ranges from 0.064 to 0.626, comparable to the values reported by Kehoe et al. (2008) in fitting Weibull functions to the acquisition of conditioned nictitating membrane responses in rabbits. This value for R^2 was often quite low because, at the behavioral asymptote, trial-by-trial response counts vary substantially (as evident in the two traces shown in Figure 2). Although the asymptote of the Weibull function accurately estimates the mean of these response counts, the function does not explain any of the variance in this noisy data, thus limiting the maximal value of R^2. This limitation is addressed in one of the analyses described below.

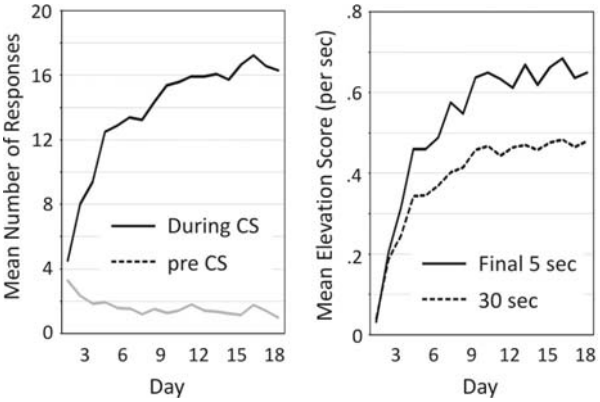

Figure 1. Left: Mean number of responses per 30-s CS or pre-CS period across 18 days of conditioning. Right: Mean elevation score, calculated as the response rate (per second) during the CS minus the pre-CS response rate, for each day of conditioning in Experiment 1. The dashed line plots the elevation score calculated using the average response rate over the entire 30-s duration of the CS; the solid line plots the elevation score for the response rate in the final 5 s of the CS presentation.

Weibull functions were used to estimate the latency for each rat to start responding to the CS, calculated as the trial on which the Weibull reached 10% of its asymptote. An estimate of the rate of learning was also obtained by calculating the number of trials taken for the Weibull to increase from 10% to 90% of asymptote. As shown in Figure 2, this was 109 trials (from trial 113 to 222) for Rat 2 and 75 trials (from trial 13 to 88) for Rat 21.

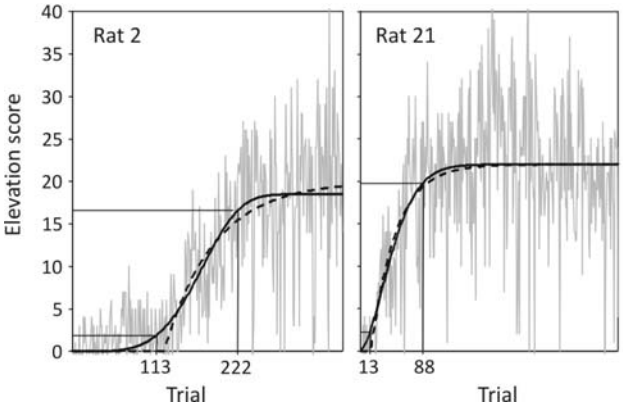

Figure 2. Gray lines plot the trial-by-trial elevation score (during-CS minus pre-CS response counts) for two rats across all 360 trials of conditioning in Experiment 1. Superimposed on these traces are the best-fitting Weibull functions (solid black line) and best-fitting exponential functions with a response threshold (dashed black lines). For the weibull functions, R^2 = 0.63 and 0.39, for Rats 2 and 21, respectively; for the exponential functions, R^2 = 0.62 and 0.38. The black horizontal lines mark the 10th and 90th percentiles for the Weibull functions, which correspond to trials 113 and 222 for Rat 2, and trials 13 and 88 for Rat 21.

Rather than attempting to show the raw response record across 360 trials for all 22 rats, Figure 3 presents the best-fitting Weibull functions to those data for each rat. There is considerable variability between rats in their estimated learning curves. The average latency to respond (to reach 10% of the asymptotic response rate) for all 22 rats was trial 24 (range = 3 to 113). In fact, with the exception of Rat 2, the other 21 rats had all started responding by the end of Day 2 (i.e., as estimated from the Weibull function for each rat, the response rate had reached 10% of asymptote by trial 40). Using Weibull functions to estimate the rate of

learning for each rat revealed that, on average, it took 129 trials for responding to increase from 10% to 90% of asymptote (this number ranged from 7 to 357 trials). Therefore, responding to the CS did not appear abruptly, but typically took more than 6 days to reach asymptote. Across the 22 functions fitted to these data, there were significant correlations between the Weibull parameters: the asymptote, λ, was negatively correlated with the slope parameter, *s* (r = -.67, *p* = .001) and positively correlated with the latency parameter, β (r = .78, *p* < .001). The correlation between *s* and β fell just short of significance (r = -.40, *p* = .06).

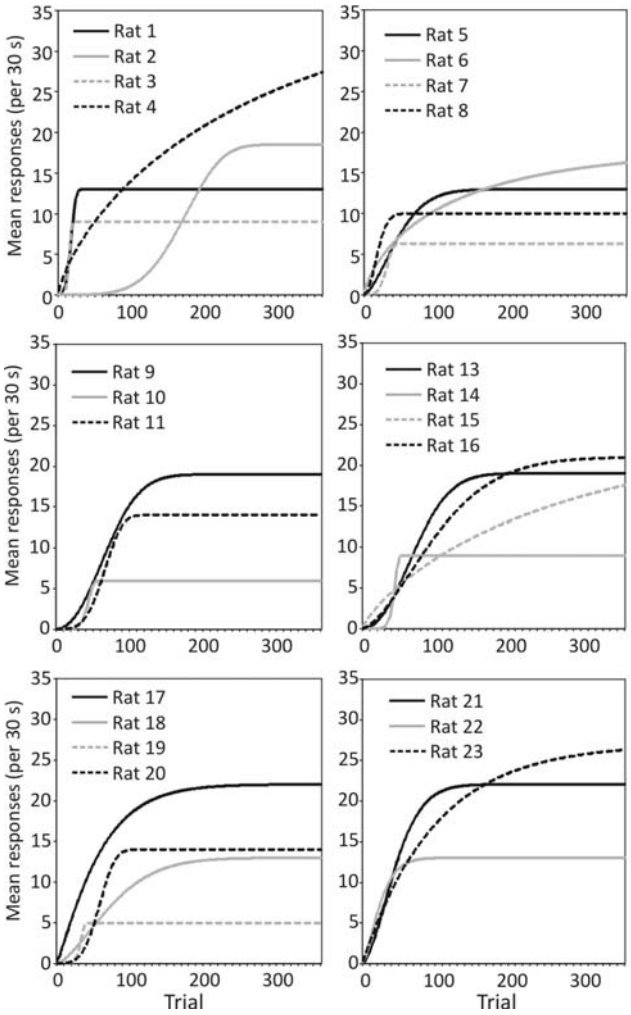

Figure 3. Weibull functions fitted to the trial-by-trial responses rates for each rat (except Rat 12) in Experiment 1.

The above analysis fitted Weibull functions to elevation scores calculated by subtracting the pre-CS response count from the response count during the CS for each trial. This analysis assumes that conditioned responding evoked by the CS is added to baseline responding, as measured in the pre-CS period. The importance of this assumption is most acute when attempting to measure conditioned response strength at the very beginning of training because, if pre-CS response counts are not subtracted, then response rates during the CS start well above zero. This is implausible as a measure of conditioning strength for a novel CS, and particularly problematic when attempting to fit any sort of acquisition function (including the Weibull) which assumes a starting value of zero. Nonetheless, this assumption may have consequences for measurement of the learning rate because, as is evident in Figure 1, the pre-CS baseline responses decline across the course of training, which will increase the number of trials across which the elevation scores rise. To take account of this possibility, Weibull functions were fitted to data in which the elevation score was calculated by subtracting the response count on each trial by a fixed baseline value calculated as the average pre-CS response count on Day 1 of training. Subtracting this single pre-CS value avoided the possibility that the rate of change in responding across trials was confounded by changes in the baseline response rate, yet it still ensured that response strength during the CS started at zero. From the Weibull functions fitted to these elevation scores, the average latency for responding to reach 10% of asymptote for all 22 rats was trial 36 (range = 4 to 131), and it took a further 97 trials for responding to increase from 10% to 90% of asymptote (range = 4 to 355 trials). These values are slightly different from those reported above, suggesting that the decline in pre-CS responding over the first 2 days of training did bring forward the estimated time at which responding began to rise. Which estimate is more appropriate will depend on the validity of the assumption that conditioned

responding adds to the pre-CS baseline response rate. Nonetheless, both sets of data show that the rise in responding across training was extended across many trials.

Comparing Weibull and Exponential Functions

To test whether the acquisition of conditioning in individual rats is adequately described by an exponential function, we found the best-fit of Equation 2 for the elevation scores for each rat. Examples where this function has been fitted to the data for Rats 2 and 21 are shown in Figure 2. It is worth noting that this function has the same number of parameters as the Weibull function. As with the Weibull function, there were also significant correlations between the parameters used to fit Equation 2 to this data: the slope parameter, k, was positively correlated with the response threshold θ (r = -.43, p = .02) but not with the asymptote λ (r = -.38, p = .073), while θ and λ were positively correlated (r = .87, p < .001).

To assess the exponential functions described above, we compared their goodness-of-fit with those of the best-fitting Weibull functions for each rat. The average R^2 for both functions was nearly identical (mean R^2 = 0.303 and 0.300 for Weibull and exponential functions, respectively). A detailed comparison of their goodness-of-fit is shown in Panel A of Figure 4, which plots the R^2 for the Weibull against the R^2 for the exponential for each rat. As evident in the scatter plot, all points lie very close to the diagonal, confirming that both functions are consistently matched in their ability to describe the response data for all rats.

The above analysis reveals that an exponential function, when combined with a simple response threshold, is as accurate as the Weibull function in capturing the trend of the response data in this experiment. However, it is possible that a meaningful difference exists between the two functions but this difference is obscured by the low value of the R^2 statistic in many cases. To rule out this possibility, the above comparison between the exponential and Weibull

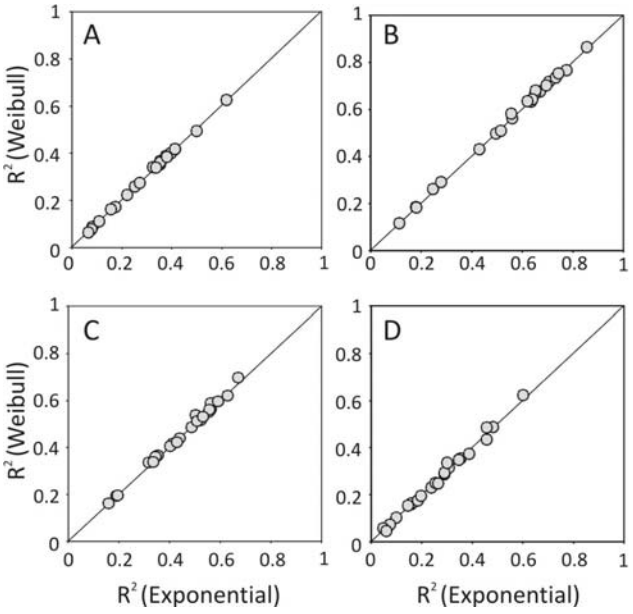

Figure 4. Scatter plots of the goodness of fit (R^2) for the Weibull function (Equation 3) plotted against the thresholded exponential function (Equation 2) for the acquisition of responding across Days 1 to 18 for each rat in Experiment 1. Panel A plots R^2 for functions fitted to the elevation score for each individual trial. Panel B plots R^2 for the same functions fitted to the elevation scores averaged across blocks of 5 consecutive trials. Panel C plots R^2 for functions fitted to elevation scores on each trial up to and including the day on which responding reached its terminal level. Panel D plots R^2 for functions fitted to elevation scores during the final 5 s of each CS presentation.

functions was repeated, but instead of fitting these functions to the response rates on each individual trial, the functions were fitted to data sets that averaged response counts across 5-trial bins. This averaging reduced much of the trial-to-trial variability in the data, and thus substantially improved the fit of both functions. This improvement is shown in Panel B of Figure 4 which plots these new R^2 values for the exponential functions against the Weibull functions for each rat. Despite the clear improvement in goodness-of-fit, there is virtually no difference in how well the two types of function fit the data (mean R^2 = 0.549 and 0.543 for Weibull and exponential functions, respectively). This confirms that the exponential

provides an accurate description of the acquisition of conditioned responding.

In a further extension of the analysis described here, the exponential and Weibull functions were fitted to a subset of trials – those covering just the initial period of conditioning when each rat's response rate was increasing towards its asymptote. That is, this analysis excludes the final portion of the data when the rat's response rate was at asymptote. This was done in order to remove a major source of variability in the data that is not relevant to the comparison between the two functions because, while the asymptote of these functions can estimate the mean of responding at asymptote, they cannot explain any of the variability around that mean. Therefore, exponential and Weibull functions have been fitted to each rat's data up to and including the day on which the response rate reached a clear asymptote (beyond which, the daily average response rate did not increase). The length of this data set varied considerably between rats: the minimum length was 40 trials (Rat 3) but included all 360 trials in cases where the response rate had not reached asymptote by Day 18 (Rats 4 and 30). Panel C of Figure 4 compares the goodness-of-fit for the two functions fitted to these data. Once again, the R^2 values for the two functions are remarkably similar (mean R^2 = 0.465 and 0.459, for Weibull and exponential functions respectively), confirming that Equations 2 and 3 are equivalent in their ability to describe the acquisition of conditioned responding in this paradigm.

The final analysis compared the exponential and Weibull functions when fitted to elevation scores confined to the final 5 s of each CS presentation. Response rates to fixed duration CSs, such as used here, typically increase across the duration of the CS, peaking shortly before the expected time of the US presentation (e.g., Holland, 2000). Averaging or summing responses across the entire duration of the CS could obscure important details of response acquisition that reflect learning about the specific time of US occurrence (Balsam, Drew, & Yang, 2002; Delamater & Holland, 2008; Gallistel & Gibbon, 2000). Thus the acquisition curve for responses made near the end of the CS may differ from that observed when averaging across the entire 30 s of the CS. Indeed, such a difference is apparent in the right panel B of Figure 1 which plots the mean elevation score for the final 5 s and for the entire 30 s of the CS presentation across each day of conditioning. The response rate for the final 5 s of the CS increased more quickly and to a higher asymptote than the response rate averaged across the entire 30-s duration of the CS. Nonetheless, when using the Weibull function to estimate the latency for responding to appear, and the rate at which it increased thereafter, these data reveal a similar pattern to that reported above for the response data from the full 30-s CS: the mean latency for responding to reach 10% of asymptote was 23 trials (range = 3 to 85), and the mean number of trials for responding to increase from 10% to 90% of asymptote was 116 (range = 21 to 475). Further, when comparing exponential and Weibull functions in their fit to the trial-by-trial response rates during the final 5 s of the CS, both functions were equivalent (both mean R^2s = .269), as shown by the scatter plot of their R^2 values in Panel D of Figure 4.

Change point analysis

The individual subject analysis described above was conducted because group-averaged data can disguise abrupt changes in responding in the response patterns of individual subjects if the point of change in responding occurs at different times between rats (Gallistel, et al., 2004). A learning curve that attempts to show the average rate of change in conditioned responding over time must align the data for each individual subject according to the time at which responding begins to rise. Gallistel et al. (2004) have described an algorithm for identifying the change point in the data record of individual subjects. This algorithm identifies

the location of any inflexion in the cumulative response record, and therefore pinpoints the trial on which there was an abrupt change in the response rate. For the analysis here, we have used the suite of Matlab program files made available by Gallistel et al. (2004), downloaded from the *Proceedings of the National Academy of Sciences, USA* website where the paper was published. These programs find change points according to a user-defined significance threshold, and therefore multiple change points can be located within a single response record. In order to identify a single "principal" change point, we repeated the algorithm while systematically increasing the significance threshold until a single increasing change point was identified for each rat (very occasionally the most significant change point would occur when the rat's response rate would drop, but we ignored such change points and confined our analysis to change points where there was a rise in response rate). Following Morris and Bouton (2006), we aligned the response record of all rats according to their change points. To remove inter-rat differences in the overall level of responding, we also normalized each rat's response record by dividing the elevation score on each trial by the asymptote of the best-fitting Weibull function. Panel A of Figure 5 shows the average across all 22 rats for the aligned and normalized response records. The figure shows the average normalized response rates beginning 14 trials before the choice point and 156 trials after it – this range includes all trials for which the records of all 22 rats overlap. There is an abrupt increase in responding from the change-point trial (trial 0 in the figure) to the very next trial, similar to that reported by Morris and Bouton.

The step-like increase in responding at the change point would appear to contradict the prediction of a gradual increase in conditioning strength, and would thus constitute evidence against incremental models of learning. However, it is possible that this abrupt change in the response record is a product of the algorithm

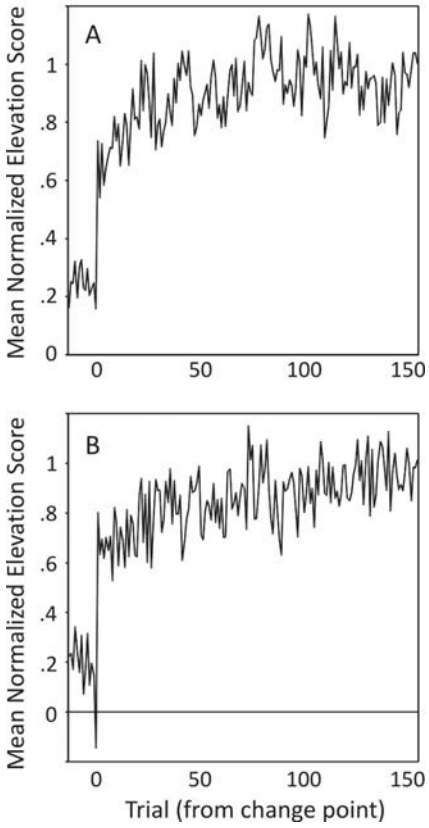

Figure 5. Panel A: Elevation scores on individual trials averaged across all 22 rats in Experiment 1. The data were aligned by their principle change point in the response record as calculated by the algorithm proposed by Gallistel et al. (2004). The data for each rat were normalized by dividing the value on each trial by the terminal response rate estimated from the asymptote of the best-fitting Weibull function. This analysis reveals a sharp step-like rise in response rate immediately after the change point. This apparent discontinuity in the response rate is replicated in the simulated data shown in Panel B. These data were generated from the best-fitting exponential functions (Equation 2) for each rat, to which normally-distributed random jitter was added.

that identifies the change point, rather than reflecting an abrupt change in the processes that underlie responding. The change point algorithm will be attracted to locations in the response record where there is a large difference in response count between two consecutive trials, yet such differences may frequently arise from random fluctuations in

the trial-to-trial response pattern of the rat. When response records are aligned to this change point, this could reveal a large and consistent difference between trials either side of the change point simply because of the increased likelihood of a random fluctuation between consecutive trials at the location of the change point. To investigate this possibility, I have conducted a simulation that is presented in Panel B of Figure 5. This simulates response data using the best-fitting exponential functions for each rat: on each "trial" the associative strength was estimated from the best-fitting exponential function, and random jitter was added to this value. The jitter was a random number, selected from a normal distribution with mean of zero and standard deviation equal to half the terminal strength of the exponential function. (I used this approximation of the random variance in the response rates because analysis of the rats' behavioral data indicated that the standard deviation of each rat's response rate was typically equal to half the asymptotic response rate, and usually did not change systematically across the course of conditioning.) Having generated variable response rates from the exponential functions for each rat, I subjected these simulated data to the change point analysis proposed by Gallistel et al. (2004), before normalizing and aligning all 22 simulated records by their change points. The average of these aligned simulated data is shown in Panel B of Figure 5, and clearly resembles very closely that shown in Panel A of the same figure. However, the step-like increase in the simulated data plotted in Panel B does not reflect any discontinuity in the underlying behavioral process, but rather reflects the combination of a gradual continuous rise in conditioning strength combined with random variability in output.

Discussion

This experiment fitted cumulative Weibull functions to the trial-by-trial response records of individual rats to estimate their rate of acquisition of conditioned responding. Following the suggestion by Gallistel et al. (2004), this function was used to calculate each rat's latency to start responding, as the point at which the Weibull function reached 10% of its asymptote, and the rate at which responding then increased towards its asymptote, as the number of trials for the function to rise from 10% to 90% of asymptote. Responding emerged within the first 2 days (40 trials) in 21 of 22 rats, and increased relatively gradually thereafter, taking on average 129 trials to climb from 10% to 90%. This rate of acquisition varied greatly between rats, ranging from 7 to 357 trials. Nonetheless, the values are much larger than those reported by Gallistel et al. (2004) in their survey of acquisition data from several conditioning paradigms, but they are similar to those reported by Kehoe et al. (2008).

The experiment also sought to determine whether the rate of learning could be effectively described by a simple difference term. This was confirmed when a modified linear exponential function (Equation 2) was shown to be as accurate as the Weibull function in fitting the behavioral data of individual rats. However, when examining the rate of increase in conditioned responding at the so-called change point (Gallistel, et al., 2004), there was a sharp step-like rise in response rate. This discontinuity in the acquisition function would be difficult to reconcile with an incremental learning process. But further analysis revealed a very similar step-like rise at the change point in a set of simulated data generated by an exponential function with random variance added to its trial-by-trial output. This demonstrates that the abrupt jump in response record at the change point does not necessarily reflect a discontinuity in the underlying behavioral process. Thus the data from this experiment confirm that a simple difference term, of the sort presented in Equation 1, provides an accurate description of the rate of learning for each individual rat, consistent with the argument that learning involves the gradual accumulation of conditioning strength over trials.

Experiment 2

In Experiment 1, the rate at which rats acquired conditioned responding was successfully described by a linear difference rule in which learning on each trial is proportional to the difference between what has already been learned about the CS-US association and the maximum that can be learned about that association (Equation 1). Experiment 2 provides a further test of the adequacy of this rule in describing the rate of learning. Rats were conditioned concurrently with two compound CSs, one of which ("CRf") was reinforced with food on every presentation, while the other ("PRf") was reinforced on one in three presentations. (Audiovisual compounds were used for the two CSs so they could be more effectively matched in salience, thereby reducing differences in learning rates.) An illustration of the difference in V between CRf and PRf CSs based on Equation 1 is shown in the left panel of Figure 6: the saw-tooth acquisition function for PRf reflects the trial-by-trial rises and falls in V following each reinforced and non-reinforced trial. (Note that, in Experiment 2, reinforced and non-reinforced trials were randomly shuffled, unlike the simulation shown in Figure 6.) The trend of the function for PRf can be well approximated by the integral of Equation 1, as shown by the smooth gray line passing through the saw-tooth function in Figure 6. Therefore, the response data for CRf and PRf compounds have been analysed using the procedure described for Experiment 1, comparing Equations 2 and 3 in their ability to describe the acquisition of responding.

The analysis of the data in this experiment is extended to examine three properties concerning the relationship between the CRf and PRf CSs, as anticipated by models that equate learning with an error term. The first issue relates to the response threshold, θ. The logic of this threshold is that it reflects a property of the response system – that V must exceed some value before learning can be expressed in performance. As such, the value of θ should not depend on the CS itself or its V. In other words, whatever value θ might take for a given rat, it should apply to both CRf and PRf compounds (as illustrated in Figure 6). Therefore, when fitting thresholded exponential functions (Equation 2) to the behavioral data of individual rats in this experiment, θ should take the same value for both CRf and PRf data sets.

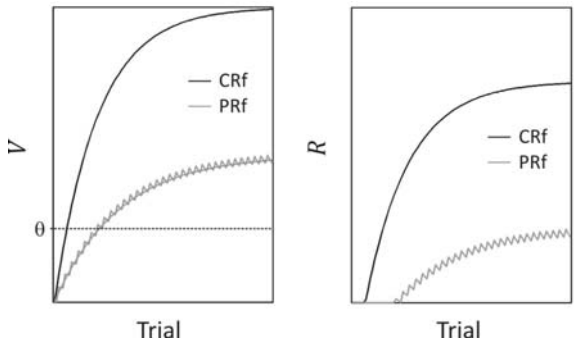

Figure 6. Left: Plot of associative strength (V), as defined in Equation 1, for two CSs, one of which (CRf) is reinforced on every trial and the other (PRf) is reinforced on one in every three trials. The saw-tooth PRf trace shows the trial-by-trial rises and falls in V across reinforced and non-reinforced trials. The smooth line superimposed on this trace shows the trend in growth of V based on the integral of Equation 1. The dotted line represents a hypothetical response threshold (at θ), responding is only observed when V is above this threshold. Right: Plots of response strength (R) for the same two CSs, based on values of V above the response threshold, as defined in Equation 2.

The second issue concerns a prediction about the terminal associative strength, V_t, of the PRf compound. For the CRf compound, V_t will equal λ. For the PRf compound, V_t will be less than λ due to a consistent decrease in V on every non-reinforced presentation (as simulated in the left panel of Figure 6). From Equation 1 is possible to specify the terminal strength of PRf relative to λ because V_t will be reached when the rise in V on each reinforced trial is matched by the fall in V on intervening non-reinforced trials. This can be expressed formally as

$$k_1 \cdot [\lambda - V_t(PRf)] \cdot r = -k_0 \cdot (0 - V_t) \cdot (1 - r)$$

where V_t is the terminal conditioning strength of PRf, and r is the reinforcement rate of PRf, and k_1 and k_0 are learning rates for reinforced and non-reinforced trials, respectively (i.e., in the terms of Rescorla & Wagner, 1972, the difference between k_1 and k_0 reflects differences in β for reinforcement versus non-reinforcement). Re-arranging the above equation, and substituting V_t (CRf) for λ, gives us the following relationship between terminal conditioning strength for the PRf and CRf compounds:

$$V_t(PRf) = \frac{r \cdot k_1}{[r \cdot k_1 + (1-r) \cdot k_0]} \cdot V_t(CRf) \quad (4)$$

The third aspect to the relationship between the CRf and PRf CSs, as anticipated by error-correction models, concerns the learning rate k. Notwithstanding the predicted difference in terminal response rates for CRf and PRf, from Equation 1 it should be possible to specify the rate at which the two compounds approach those behavioral asymptotes. For CRf, the learning rate, k_{CRf}, is simply k_1 above because every CRf trial is reinforced. For PRf, the learning rate, k_{PRf}, is the weighted average of k_1 and k_0, with the respective weightings being equal to the proportion of trials that are reinforced and non-reinforced. That is, $k_{\text{PRf}} = r \cdot k_1 + (1\text{-}r) \cdot k_0$. The right hand side of this equation is the denominator of Equation 4. Therefore, substituting k_{CRf} for k_1, we can define k_{PRf} as

$$k_{\text{PRf}} = k_{\text{CRf}} \cdot r \cdot \left[\frac{V_t(CRf)}{V_t(PRf)}\right] \quad (5)$$

This is useful because, even though we cannot specify *a priori* the relationship of k_0 to k_1, Equation 5 specifies the relationship between k_{PRf} and k_{CRf}, and therefore it should be possible to use Equation 2 to model the data for both CRf and PRf without using independent learning rate parameters for each CS.

To test the three relationships described above, Weibull and exponential functions were once again fitted to the behavioral data. Independent Weibull functions were fitted to the CRf and PRf data; that is, separate functions were fitted to both sets of data allowing all three parameters to vary independently (thus the full set of data were fitted with two Weibulls, using a total of six free parameters). The estimated asymptotes of these functions were then compared to test for the predicted difference in terminal response strength between the CRf and PRf compounds. Next, for each rat the combined fit of the two Weibull functions, calculated as a single R^2, was compared to the combined fit of two exponential functions. In the first instance, the combined Weibull fits were compared with the combined fits of two exponential functions for which all three parameters were allowed to vary independently (thus fitting the full data set with a total of six parameters). Then, to examine each of the three relationships described above, the Weibull fits were compared with those of two exponential functions that were constrained to a smaller set of parameters. In the first analysis, the two exponential functions were constrained to share a single response threshold, θ. According to linear difference models, the fit of these two exponentials, with a total of 5 parameters, should be equivalent to that of the two fully independent Weibulls. This was followed up by two further analyses that limited the exponential functions to just 4 free parameters. In both analyses, the two exponentials continued to share a single value for θ. In one analysis, the two functions also shared the same terminal strength (V_t), which should, according to linear difference models, reduce the accuracy with which they can fit the data. In the other analysis, the two rate parameters, k, were constrained such that k_{PRf} was not a free parameter but was defined according to Equation 5. According to the linear difference rule, despite this constraint to k_{PRf}, the fit of these exponential functions should match that of the Weibull functions.

One limitation of the analyses just described is that they compare functions that have different numbers of free parameters. This is important

because a function with more parameters is at greater risk of "over-fitting" the data, that is, explaining noise rather than meaningful variance. This problem can be overcome by comparing the functions in terms of a Bayesian Information Criterion (BIC) score (Schwarz, 1978). Accordingly, further analyses were conducted that compared the BIC scores for Weibull and exponential functions fitted to the behavioral data.

Methods

Subjects and Apparatus

Seventeen experimentally naive male rats (200-280g), of the same strain and source as Experiment 1, were housed in the manner described above. They were trained in the same chambers, with the same four stimuli, as in Experiment 1. The stimuli were presented as simultaneous compounds: the steady light and piezo buzzer were combined as one compound, the flashing light and white noise were combined as the other compound. The allocation of these two compounds to the two conditions of the experiment was counterbalanced between rats.

Procedure

Rats received magazine training as in Experiment 1. They then received 30 days of conditioning with two compounds, with each daily session lasting 90 min. The sessions consisted of randomly intermixed 30-s presentations of two compound stimuli. One compound (CRf) was presented 18 times, and each presentation was followed by the delivery of a single food pellet. The other compound (PRf) was presented 18 times, and one third of these presentations were followed by food. The interval between CS presentations varied randomly, with an average 120 s (and minimum of 50 s). Across all 30 days, the number and duration of photo-beam interruptions by head entry into the magazine was recorded during each 30-s stimulus and during the 30-s pre-stimulus interval.

Results

For each rat, the number of responses made during presentations of each compound (CRf and PRf) and the pre-CS period were recorded. The daily means across all rats are shown in Figure 7. It is clear that responding to CRf increased more than responding to PRf. Statistical analyses confirmed these observations. Responding to CRf was greater overall than to PRf ($F_{1,16}$ = 74.28, p < .001). There was a significant linear trend in responding to both compounds over days ($F_{1,16}$ = 19.33, p < .001), and a significant quadratic component to this trend over days, $F_{1,16}$ = 36.60, p < .001) confirmed that responding reached an asymptote. There was no difference in linear trend over days between the two compounds ($F_{1,16}$ < 1), but there was a significant difference in their quadratic components ($F_{1,16}$ = 43.26, p < .001) confirming that responding to CRf increased more sharply than did responding to PRf.

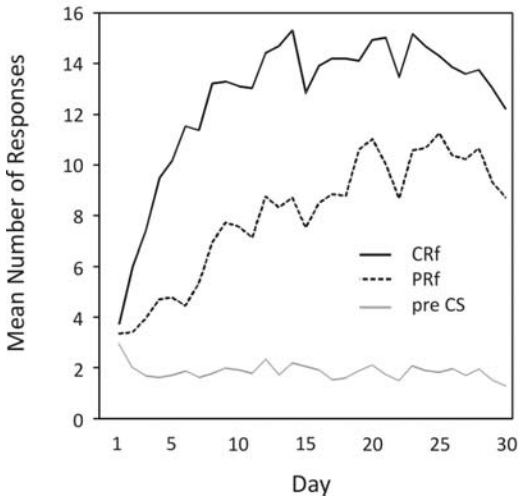

Figure 7. Mean number of responses per day during presentations of the CRf compound and the PRf compound, as well as during the pre-CS interval.

As for Experiment 1, Weibull functions were fitted to the trial-by-trial elevation scores for each individual rat, finding the best-fitting functions for each compound. These functions confirmed that the asymptote for the CRf

compound (mean = 12.59) was greater than the asymptote for the PRf compound (mean = 9.56), t_{16} = 4.19, p < .001. The two functions also differed in their latencies to reach 10% of the asymptote: on average this point was reached by the 21st CRf trial and by the 47th PRf trial, t_{16} = 2.90, p = .010. The difference in latency to respond was confirmed by the change point analysis used in Experiment 1, which established that the change point for responding to CRf (mean = trial 83) was significantly earlier than for PRf (mean = trial 153), t_{16} = 3.10, p = .007. The two Weibull functions also differed in the rate at which they increased towards their asymptote: taking on average 114 CRf trials and 247 PRf trials to increase from 10% to 90% of asymptote, t_{16} = 3.76, p = .002.

As for Experiment 1, the best-fitting exponential function was identified for each rat's data with each compound. For the first stage of this analysis, separate functions (with independent parameters) were found for the CRf and PRf compounds. An overall R^2 was calculated based on the proportion of total variance in the response data that was accounted for jointly by the two functions. This was compared to the combined fit of the two Weibull functions described above. The comparison between the functions is shown in Panel A of Figure 8, which plots the overall R^2 for the exponential against the overall R^2 for the Weibull. It is clear that the quality of fit for the two functions was very similar since all points lie on or very close to the diagonal.

Further analyses were conducted that compared the exponential and Weibull functions, but with specific constraints on the exponential functions for the CRf and PRf data. The first of these incorporated the constraint that the two exponential functions share a single threshold value, θ. Thus the two exponential functions, with a total of five free parameters, were compared against the two Weibull functions with a total of six free parameters. The scatter plot of the R^2 values is shown in Panel B of Figure 8. Once again, the R^2 values for all rats were close to or located on the diagonal, indicating that the exponential functions with common threshold provided as accurate a description of the behavioral data as that provided by the two fully-independent Weibull functions.

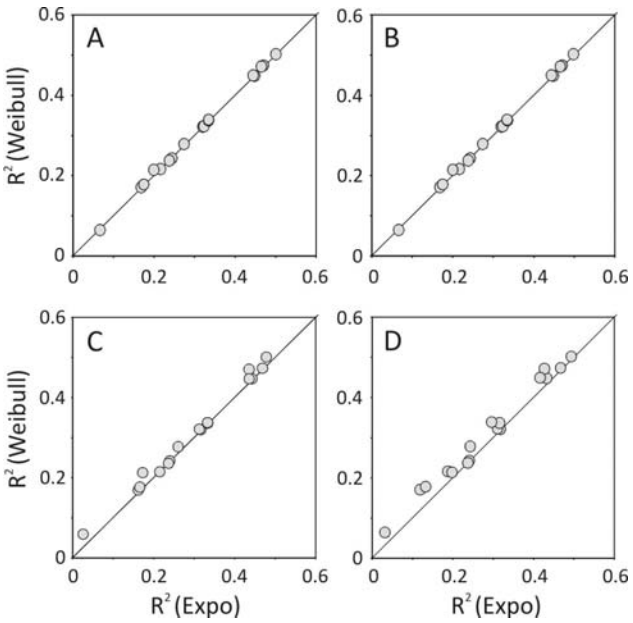

Figure 8. Four scatter-plots of the R^2 for the two best-fitting Weibull functions (Equation 3) against the R^2 for the two best-fitting exponential functions (Equation 2) for the combined CRf and PRf response data for each rat in Experiment 2. In all four plots, both Weibull functions were fully independent (thus the data were modeled with six free parameters). In **A**, the two exponential functions had fully independent parameters. In **B**, both exponential functions shared a single response threshold, θ, but independent asymptotes, λ, and rate parameters, k. In the lower plots, the two exponential functions had a total of four free parameters: they shared a single value of θ, and either had non-independent values for k (**C**) or had a single λ (**D**).

The above analysis was pursued a step further, comparing two independent Weibulls against two exponentials that shared a single θ, and had non-independent rate parameters, where k_{PRf} was defined in terms of k_{CRf} according to Equation 5. Panel C of Figure 10 shows the

scatter plot of the combined R^2 values. On this occasion, the R^2s for numerous rats deviated from the diagonal, with slightly higher values for the Weibull functions than for the exponential functions. As a final analysis, the response data for the CRf and PRf compounds were fitted with two exponential functions that shared a single θ and single λ, but had independent ks. This comparison is shown in the scatter plot in Panel D of Figure 8. In the majority of cases, the R^2s were higher for the Weibull functions than for the exponential functions.

The above analyses suggest that two exponential functions with a common response threshold are as accurate in describing the behavioral data as two fully independent Weibull functions, whereas two exponential functions with non-independent rate parameters, or with a common asymptote, provide a poorer description of the data. However, before reaching any such conclusions, it is important to take account of the difference in number of parameters between the functions being compared. That is, in the last three comparisons, the Weibull functions had more free parameters than the exponential functions. These extra parameters put the Weibull functions at greater risk of over-fitting the data. To overcome this problem, the functions were compared using BIC scores (Schwarz, 1978) that take into account the number of parameters each function uses to model the data. The general form of this score is

$$\mathrm{BIC} = -2 \cdot \ln(L) + p \cdot \ln(n)$$

where L is the maximum likelihood of the function given the data, p is the number of parameters in the function, and n is the number of data points. If we assume that the error variance in the data is normally distributed, the above formula can be simplified to

$$\mathrm{BIC} = n \cdot \ln(RSS) + p \cdot \ln(n)$$

where RSS is the sum of squared residuals for the model being tested (Burnham & Anderson, 2004; Ludden, Beal, & Sheiner, 1994). (The full calculation of BIC includes an additional parameter that estimates the population variance from the sample, but this parameter has been subtracted out of the formula used here because, as an added constant, it should be irrelevant to any comparison between different BIC scores based on the same data.) For each rat's data, the BIC score was computed for both Weibull and exponential functions. When comparing BIC scores it is the size of the difference, not the ratio, that matters, and the model with the smaller BIC score is preferred. Accordingly, Figure 9 plots the differences between the two BIC scores (ΔBIC) for each rat. As calculated here ($BIC_{exponential} - BIC_{Weibull}$), a positive value for ΔBIC indicates superior performance of the Weibull functions.

Figure 9 shows the ΔBIC scores for three comparisons between the fit provided by two independent Weibull functions and the fit provided by two exponential functions. In the first comparison (on the left of Figure 9), the Weibulls are compared with two exponentials using a single θ but independent k and λ. Most of these ΔBIC scores are negative (mean = -5.11), suggesting an advantage for the 5-parameter exponential functions over the 6-parameter Weibulls. A paired student *t*-test confirmed that there was a significant difference between the BIC scores for the exponential and Weibull functions, $t_{16} = 3.57$, $p = .003$.

In the second comparison (shown in the middle of Figure 9), the Weibull functions are compared with two exponentials that share a single θ and have non-independent ks (k_{PRf} is defined according to Equation 5), but with independent λs. These ΔBIC values are distributed around zero (mean = 3.06), as confirmed by statistical analysis showing that the difference in BIC scores between Weibull and exponential functions is not significant, $t_{16} < 1$.

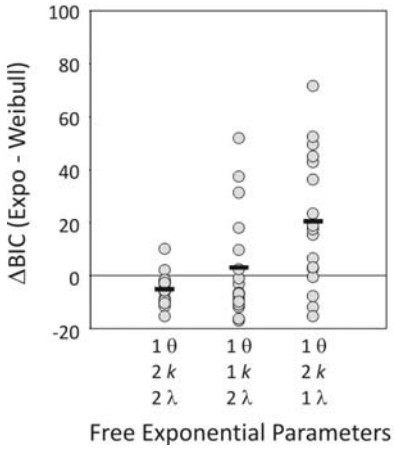

Figure 9. Plotting the difference in Bayesian Information Criterion (ΔBIC) scores between the best-fitting exponential and Weibull functions in Experiment 2. Each gray dot represents the ΔBIC for a single rat, calculated using the combined CRf and PRf response data. These are shown for three separate analyses that used different numbers of free parameters when fitting the exponential functions. The exponential functions either (1) shared a single response threshold, θ, but had independent rate parameters, k, and asymptotes, λ, (2) had a single θ and non-independent ks, but had independent λs, or (3) shared a single θ and a single λ, but had independent ks. When comparing BIC scores, the model with the lower BIC is favored, and therefore a positive ΔBIC indicates superior performance of the Weibull functions than the exponential functions. The black horizontal bars show the mean ΔBIC for each analysis.

In the third and final comparison (shown on the right of Figure 9), the two Weibull functions are compared with two exponential functions that share a single θ and a single λ, but independent ks. In the large majority of cases, the ΔBIC was positive (mean = 20.55), and the overall difference between the BIC scores was significant, $t_{16} = 3.35$, $p = .004$. This confirms that the response data in this experiment are not adequately explained by a model that assumes that the CRf and PRf compounds reach the same terminal response rate.

Discussion

This experiment has confirmed that the trial-by-trial change in conditioned responding for data from individual rats can be described by an exponential function incorporating a response threshold (Equation 2) as accurately as by a Weibull function. This was true both for a continuously reinforced compound (CRf) and a partially reinforced compound (PRf). Thus these data, like those of Experiment 1, support the claim that learning is effectively described by an error term in which associative change is proportional to the difference between the current associative strength of a CS and the maximum strength sustained by the US.

This experiment presented additional tests of the manner in which the error term captures learning. The rule predicts a higher terminal response rate to a continuously reinforced CS than to a partially reinforced CS, and this prediction was supported by the data presented here. The rule also predicts that the appearance of responding to each CS should be subject to the same response threshold, and that the rate of associative change for the two CSs should be related according to Equation 5. The analysis presented here was consistent with both of these predictions.

General Discussion

Two experiments examined in detail the rate of acquisition of conditioned responding by analyzing response rates on each trial for individual rats. Following the arguments made by Gallistel et al. (2004), the central tendency of each rat's responding over time was estimated using a cumulative Weibull function fitted to the data record of each individual rat. This function is well suited to the task because it can describe either gradual learning curves or very abrupt transitions in response rate, and can equally describe a rise in responding that appears at the outset of conditioning or after a

lengthy delay. Thus the function itself is "neutral" with respect to these details of the shape of the acquisition function.

Estimating learning rates and latencies from the Weibull function

For the data from each rat, the best-fitting Weibull function was used to provide an estimate of each of the two variables just described. The latency for responding to emerge was estimated by calculating the number of trials required for the function to reach 10% of its terminal height (asymptote). The learning rate was estimated as the number of trials required for the Weibull function to rise from 10% to 90% of its asymptote. This analysis was first applied to the data from Experiment 1 in which rats were trained with a single CS that was reinforced on every trial. It took on average 24 trials for responding to reach 10% of asymptote, and a further 129 trials for responses to rise to 90%. In Experiment 2 rats were trained with two CSs: one (CRf) was continuously reinforced, as in Experiment 1, and the other (PRf) was partially reinforced (on one in three trials). It took 21 and 47 trials respectively for responding to CRf and PRf to reach 10% of its asymptote, and a further 114 and 247 trials for responding to rise to 90%. These values for estimated learning rates are much larger than those reported by Gallistel et al. (2004) in their survey of acquisition data from several conditioning paradigms, but are comparable to those reported by Kehoe et al. (2008). Such prolonged periods of acquisition are consistent with the conventional view that treats learning as a gradual accumulation of conditioning strength (Hull, 1943), but are not consistent with models in which conditioned responding emerges abruptly when conditioning exceeds a decision threshold (e.g., Gallistel & Gibbon, 2000). To explain such protracted acquisition, such models must assume there is substantial trial-to-trial variability in the operations that underlie the decision, such as the value of the threshold or the evidence that is compared against the threshold. Whether the rate of change in responding reported here can be explained by variability of this sort will depend on the details of the model in question.

In analyzing the acquisition of autoshaped key-pecking in pigeons, Gallistel et al. (2004) reported there was little or no correlation between key parameters in the Weibull functions fitted to their data. In particular, the parameter β in Equation 3, that reflects the latency for responding to emerge, was not correlated with either λ (the asymptote) or *s* (the relative slope of the acquisition curve). Thus they concluded that the onset latency did not predict either the relative rate at which responding increased or the eventual level of responding. However, the data from Experiment 1 revealed significant positive correlations between β and λ, and between *s* and λ. Thus in the present data, a longer latency to respond, and a steeper rise in responding, were each associated with a higher terminal levels of responding. These relationships are not anticipated by the decision-based acquisition processes.

Comparing cumulative exponential and Weibull functions as descriptions of the learning curve

The primary goal of these experiments was to determine whether the rate of learning could be effectively described by a difference or error term (Equation 1) of the sort incorporated into most associative models of conditioning. However, as noted above, conditioned responding did not appear immediately after the first conditioning trial, even though, according to the error term, the greatest increments in conditioning strength should occur in the first few trials. Thus it was necessary to modify the learning rule to capture more adequately the pattern of responding over trials. The analysis chosen here incorporated the suggestion (Hull, 1943; Spence, 1956) that responding is subject to a performance threshold – conditioned responding only appears once associative

strength exceeds this threshold. This modified rule, expressed as a thresholded exponential function (Equation 2), was fitted to the response data for each rat. In both experiments, the exponential was as good as the Weibull function in fitting the data. This is important because the Weibull is well equipped to capture abrupt changes in responding, particularly when they occur after a delayed onset, by allowing the parameter *s* to take a value much larger than 1. The fact that the thresholded exponential function fitted the acquisition data as well as the Weibull demonstrates that the exponential function does describe the emergence of conditioned responding even when the appearance of responding is delayed. This implies that the behavioral data of individual rats did not deviate from the acquisition curve predicted by incremental models of learning.

A danger when attempting to fit a particular model to behavioral data is that, with enough parameters, the model's equations can fit almost any pattern of data. On this issue, Gallistel et al. (2004) have pointed out that an incremental learning process can be made to produce step-like changes in responding if one assumes that the behavior is constrained within a narrow performance range – the transition from no response to maximum response can appear abrupt if that response is "letter-boxed" between a high behavioral threshold and a low response ceiling. In effect, any discontinuity in the acquisition curve is attributed to non-linearity in the rule for mapping conditioning strength to response strength. But using such performance rules to describe behavioral data can undermine the explanatory value of an incremental learning model because it admits that the very predictions the model makes about the nature of learning may not be evident in behavior and thus cannot be falsified. However, this charge is not applicable in the present case. The incremental learning model used here did incorporate a behavioral threshold, but not a performance ceiling, and so when fitting the model to the data the terminal response rate was modeled by the asymptote of learning. In Experiment 1, the data for 9 out of 23 rats was modeled using a high behavioral threshold (above 60% of asymptote) and high asymptote, in order to achieve a sufficiently steep rise in responding. But for the remaining 14 rats, the threshold was low (on average, 22% of asymptote) such that there was a wide range of response rates across which responding increased gradually. This meant that, across the entire sample of rats in Experiment 1, there was a strong positive correlation between threshold and asymptote, and also between threshold and learning rate. But more importantly, the majority of rats showed a gradual learning curve that could be modeled effectively by Equation 2 without relying on a high behavioral threshold.

In sum, the analysis presented here shows that conditioning data of individual rats can be equally well described by the conventional incremental learning curve as by a Weibull function that more readily accommodates discontinuous acquisition curves. Of course, this comparison may be taken as evidence in support of the incremental model of learning, or as reason to question the claim (Gallistel, et al., 2004) that the Weibull function represents a better description of conditioning data. At the very least, the present findings challenge the assertion that the acquisition of conditioned responding is poorly described by incremental learning models when the analysis is conducted at the level of individual subjects rather than group averages (Gallistel, et al., 2004).

Layered associative networks

It is worth pointing out that the notion of a response threshold is not the only mechanism by which associative models that use an error term can account for the sigmoid shape of acquisition functions. Response acquisition would be sigmoid if the strength of responding is determined not by a single associative link, as implied by the associative analysis presented thus far, but by multiple links connected in series. Such "layered" associative networks

have proved popular among computational models in cognitive science (Rumelhart, Hinton, & Williams, 1986), and can provide simple but powerful solutions to problems in associative learning such as learning-to-learn and evidence for configural encoding (Kehoe, 1988). They are relevant to the present discussion because the serial arrangement of associative links connecting a CS to the response output means that response strength depends on the product (not sum) of those links. Therefore, even if each link's growth is determined by the error-correction algorithm described in Equation 1, the product of their exponential growth functions is sigmoid. This is illustrated in Figure 10, which plots the response strength, R, calculated as the product of p identical exponential growth functions, as shown in Equation 6.

$$R_t = \lambda \cdot \left(1 - e^{-k \cdot t}\right)^p \qquad (6)$$

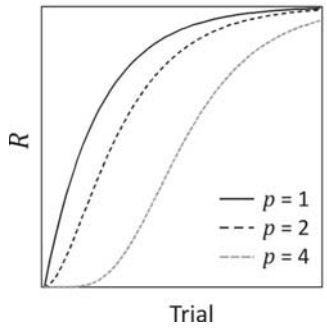

Figure 10. Response strength (R) across trials calculated according to Equation 6, with λ = 1 and k = 0.1. In the three curves shown, the cumulative exponential functions were raised to the power, p, in order to model the growth of R arising from p associative links connected in series.

To test how well this type of associative structure describes the acquisition of responding in the present experiments, an analysis was conducted that found the best fit of Equation 6 to the response data of each individual rat in Experiment 1 (as had been done for the Weibull and thresholded exponential functions). The fits to each rat's data obtained with Equation 6 (mean R^2 = 0.304) were as good as those obtained using the Weibull function (mean R^2 = 0.303) or thresholded exponential function (mean R^2 = 0.300), using the same number of free parameters. This confirms that conditioning can be successfully described by a layered associative model in which each associative link grows according to the error-correction rule defined in Equation 1.

Change point analysis

The data from Experiment 1 were subjected to a further analysis that examined the rate of increase in conditioned responding at the so-called change point – the trial on which the cumulative response record shows the greatest change in slope, corresponding to the point at which there was the largest sustained increase in response rate (Gallistel, et al., 2004). Morris and Bouton (2006) used this procedure to analyze acquisition data from an experiment similar to that described here. They reported that, when the rats' response records were aligned according to their change points, there was a sharp step-like rise in response rate at the change point itself. A similar abrupt rise in responding was observed here when the same analysis was applied to the data from Experiment 1. This discontinuity in the acquisition function would be very difficult to reconcile with a cumulative learning process, but is consistent with the suggestion that the change point corresponds to the trial on which each subject in a conditioning experiment reaches a discrete decision threshold to respond (Gallistel, et al., 2004). However, further analysis revealed a very similar step-like rise at the change point in a set of simulated data generated by an incremental learning mechanism (Equation 2) with added random variance in its trial-by-trial output. This demonstrates that the abrupt jump in response record at the change point does not necessarily reflect a discontinuity in the underlying behavioral process, but highlights the fact that the change point analysis is sensitive to random

fluctuations in the data when superimposed on a gradual and continuous learning process. Thus the appearance of an abrupt rise in responding at the change point does not refute the argument that learning involves the gradual accumulation of conditioning strength over trials.

The relationship between CRf and PRf learning curves

Experiment 2 provided further opportunity to test the adequacy of the difference rule in explaining the acquisition of conditioned responding. As mentioned earlier, rats in this experiment were concurrently conditioned with two CSs, one (CRf) was reinforced on every presentation and the other (PRf) was reinforced on one in three presentations. Equation 2 anticipates particular relationships between the acquisition of conditioning to CRf and PRf. First, it predicts that the terminal level of responding to PRf will be lower than to CRf. It makes this prediction because conditioning to PRf will plateau when the increments in V on each reinforced trial ($k_1 \cdot [\lambda\text{-}V]$) equal the decrements in V on the intervening non-reinforced trials ($k_0 \cdot [0\text{-}V]$). The average response rates shown in Figure 7 are certainly consistent with this prediction. The prediction was also confirmed by a significant difference in asymptotes of the best-fitting Weibull functions fitted to the CRf and PRf data.

According to the logic of the response threshold, θ, incorporated in Equation 2, that threshold is a property of the response system, not the learning system, and therefore the appearance of responding to CRf and PRf should be subject to the same threshold. This means that the acquisition of responding to CRf and PRf should be successfully fitted by two exponential functions that share a single value for θ. This was confirmed when two such functions were shown to fit the data as well as two fully independent Weibull functions (i.e., the two Weibull functions had a total of six free parameters). Thus, responding to CRf and PRf can be adequately described by Equation 2 when assuming that responding to the two CSs is affected by the same performance threshold.

The third feature of the relationship between PRf and CRf, as stipulated by Equation 2, concerns the rate of learning. The learning rate parameter for PRf, k_{PRf}, can be estimated from the learning rate to CRf, k_{CRf}, as presented in Equation 5. If there is such a relationship between the two CSs, it should be possible to fit exponential functions to the data without requiring free rate parameters for each CS, but instead by fitting both functions using one free rate parameter, k_{CRf}, while defining the value of k_{PRf} according to Equation 5. When two exponential functions were fitted to the data using a total of just four free parameters (k_{CRf}, θ, λ_{CRf} and λ_{PRf}), their combined fit was slightly worse than that of the two Weibull functions. However, this difference disappeared when the fits of the exponential and Weibull functions were compared in terms of their BIC scores (Schwarz, 1978), which take into account the increased risk of "over-fitting" the data (fitting noise) with each additional free parameter that a model uses. Thus this result provides further support for the linear difference rule, from which one can derive the relationship defined in Equation 5, as an accurate description of the operations that underlie learning.

Finally, the analysis just described was also used to confirm the prediction that the terminal rate of responding to PRf would be less than that to CRf. When the data were fitted using two exponential functions that shared a single asymptote and a single θ, but different ks, the fits obtained were distinctly worse than those achieved by the two independent Weibull functions, even when the functions were compared in terms of BIC scores. Therefore, whereas the acquisition of responding to CRf and PRf can be successfully described by two exponential functions that share a common performance threshold and non-independent learning rates, it cannot be adequately

described by two exponential functions with the same asymptote.

Rate Estimation Theory

The experiments and analyses presented here were designed specifically to test how well Equation 2 serves as a description of learning. Nonetheless, certain aspects of the data do bear on an alternative account of conditioning, Rate Estimation Theory (RET), proposed by Gallistel and Gibbon (2000). One major difference between these accounts is that RET anticipates the abrupt appearance of conditioned responding whereas models that use an error term to compute learning on each trial anticipate the gradual accumulation of conditioning strength. In this respect the present data offer stronger support for error-term models than RET. A second difference between these models concerns the asymptotic level of responding to CRf and PRf in Experiment 2. As already noted, the error-term models correctly anticipate higher terminal conditioning strength for CRf than PRf. RET, on the other hand, does not anticipate this difference because, as long as the rats have reached their decision threshold to respond, the response rates to both CSs should be equivalent. However, it is possible that a difference in mean responding to the two compounds could be explained by appealing to the timing mechanism described in RET's sister theory, Scalar Expectancy Theory (SET; Gallistel & Gibbon, 2000). For example, according to SET, the rat's decision when to commence responding within a given trial is determined by its memory of the time of reinforcement. This should always approximate 30 s for CRf, but may be remembered as a multiple of 30 s for PRf, particularly if the remembered time of reinforcement accumulates across non-reinforced CS presentations, such that the rats' experiences of reinforcement during PRf will be distributed across multiple times (30 s, 60 s, 90 s etc). This could explain why the average asymptotic response rate to the PRf CS is lower than to the CRf CS – because the former includes a proportion of trials on which the rats' remembered time of reinforcement was much greater than 30 s.

A third aspect to the present data that is relevant to RET is the latency with which responding appeared to CRf versus PRf. Like models that use an error term, RET anticipates that responding to PRf will be delayed relative to CRf. In the case of error-term models, this is because it will take longer for the associative strength of PRf to reach the response threshold; for RET responding to PRf is delayed because it takes many more trials before the rate of CS reinforcement relative to the background rate of reinforcement reaches a decision threshold. More specifically, RET predicts that CRf and PRf will require the same number of reinforced trials to reach the decision threshold because they are compared against the same background rate of reinforcement. Therefore because PRf was reinforced at 1/3rd the frequency of CRf, RET predicts it will take three times longer for the rats to commence responding to PRf than to CRf. Analyses of responding to CRf and PRf in Experiment 2 confirmed that responding to PRf appeared later than responding to CRf, however the difference was smaller than anticipated by RET, the rats took about twice as long to start responding to PRf than to CRf.

Conclusions

In conclusion, the analyses of data from two experiments provided consistent support for the view that learning is an incremental process in which conditioning strength accumulates across trials according to a simple error term. The results did not reveal abrupt changes in responding across the course of conditioning, and therefore were not supportive of an alternative account of conditioning (Gallistel & Gibbon, 2000) that predicts a discontinuity in the acquisition of responding as might reflect categorical control over responding driven by a decision process.

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