Acquisition and Extinction in Autoshaping

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Acknowledgements

We are most grateful to Randy Gallistel and John Gibbon for freely sharing, prior to publication, their many ideas about timing and conditioning. We are also very grateful to Nathaniel Daw for extensive discussion; and to them, David Shanks, and three anonymous reviewers for comments. Funding is from a NSF Graduate Research Fellowship (SK) and the Gatsby Charitable Foundation.

Abstract

Gallistel and Gibbon (2000) have presented quantitative data on the speed with which animals acquire behavioral responses during autoshaping, together with a statistical model of learning intended to account for them. Although this model captures the form of the dependencies amongst critical variables, its detailed predictions are substantially at variance with the data. In the present article, further key data on the speed of acquisition are used to motivate an alternative model of learning, in which animals can be interpreted as paying different amounts of attention to stimuli according to estimates of their differential *reliabilities* as predictors.

1 Introduction

In autoshaping experiments on pigeons, birds acquire a classically conditioned peck response to a lighted key associated, irrespective of their actions, with the delivery of food (Brown & Jenkins, 1968). As stressed persuasively by Gallistel & Gibbon (2000), which we abbreviate as GG, there is substantial experimental evidence in favor of a simple quantitative relationship between the speed of acquisition in autoshaping and the three critical variables shown in Figure 1A. The first is I, the length of intertrial interval; the second is T, the time during the trial for which the conditioned stimulus (CS, a light in this case) is presented; and the third is the training schedule, $1/S$, which is the fractional number of deliveries per light (for those birds that were only partially reinforced). Here, acquisition speeds are typically measured in terms of the number of trials it takes until a certain behavioral criterion is met, such as pecking during the time the light is illuminated on three out of four successive trials (Gibbon et al, 1977, Gallistel & Gibbon, 2000).

The data in Figure 1B show that the speed of acquisition is approximately inversely proportional to I/T. More precisely, the median number, n, of *rewards* that must be presented until the behavioral acquisition criterion is met is

$$n \approx 300 \left(\frac{I}{T}\right)^{-1} \tag{1}$$

This implies that the relatively shorter the presentation of light, the faster the learning. GG make two key points about this relationship. First, the number of trials until acquisition depends on the ratio of I/T, and not on I and T separately – experiments reported for the same I/T are actually performed with I and T differing by more than an order of magnitude (Gibbon et al., 1977). Second, Figure 1C shows that partial reinforcement has almost no effect when measured as a function of the number of reinforcements (rather than the number of trials), since although it takes S times as many *trials* to acquire, there are *reinforcements* on only $1/S$

trials. This effect holds over at least an order of magnitude in S. Changing S does not change the effective I/T when measured as a function of reinforcements, so this result might actually be expected on the basis of Figure 1B.

Conversely, when rewards are no longer provided with the light, responding slowly stops, a process called extinction. The data show that about 50 rewards must be omitted before the satisfaction of an extinction criterion that the pre-extinction response rate be halved. The speed of extinction does not depend on the I/T ratio, by sharp contrast with the speed of acquisition.

These quantitative data provide a most seductive target for models of learning. Indeed, one of GG's most important contributions is to place the behavior of the animals firmly in the domain of statistical normativity. Normative models suggest that the decisions of the animals to start and stop responding are actually correct according to a well specified statistical model, given the information they have received about the relationship between stimuli and rewards, and prior expectations. Gallistel, Mark, King & Latham (2001) have shown directly that animals can be statistically optimal detectors of rate changes like those that underlie autoshaping.

GG suggest a model for acquisition and extinction data that they call rate estimation theory (RET). In RET, animals are estimating *rates* of reward delivery, and start responding to the light when it reliably signals an increase in the reward rate over the context. Equally, in extinction, they stop responding when they have observed enough omitted rewards that they can be adequately certain the reward rate associated with the light has changed.

In this paper, we we will argue that it is not possible to fit the normative statistical model underlying RET to the relevant acquisition data. Further, we construct a normative model which does match these quantitative data and also the relevant results of other experiments. In the new model, stimuli *compete* to predict the delivery of reward, on the basis of estimates of the *reliabilities* with which they make predictions. Our model incorporates quantitative versions of existing theoretical ideas about stimulus competition in classical conditioning (*eg* Mackintosh, 1975; Pearce & Hall, 1980; Grossberg, 1982).

Many of the key aspects of the data that motivated our model have been noted previously, and indeed have motivated the critical experiments such as those on fast contextual conditioning by Balsam & Schwartz (1981).

2 Rate Estimation Theory

Gallistel & Gibbon (2000) are amongst the strongest proponents of the quantitative relationships shown in Figure 1. To account for them, GG suggest that animals are estimating the underlying rates of reward in the world, *ie* the number of rewards provided per unit time in the presence of the stimuli.

Call the 'true' rate associated with the light λ_l, and that associated with the *background context* λ_b. The background context is the ever-present experimental chamber. RET uses an additive model for the delivery of reward, in that when the light is on, the true rate of reward is the sum $\lambda_l + \lambda_b$. With just the background alone, the rate is λ_b. The underlying rates are not directly observable by the animal, and so it faces the inference problem of estimating them based on the rewards and stimuli that are presented. Under RET, the rewards that are presented are allocated or apportioned between the light and the background, and the rates are estimated by dividing the total number of apportioned rewards by the total time of stimulus presentation.

To put this more formally in the context of the experiment of figure 1, the rate of reward during the background is estimated by the mean rate $\bar{\lambda}_b = n_b/t_b$, where t_b is the cumulative exposure to the background alone and n_b is the number of rewards apportioned to the background during this time. In the experiment, no rewards are actually apportioned to the background, since their occurence is tied to the light. However, it cannot safely be concluded that the background's mean rate is 0. Rather, this only justifies that the estimated mean rate is no higher than the reciprocal of the total exposure to the background, $\bar{\lambda}_b = 1/t_b$, and RET uses this conservative estimate for $\bar{\lambda}_b$. In n trials, $t_b = nI$. A standard Bayesian treatment of inference in these circumstances would lead to a similar conclusion.

Since RET uses an additive model for the delivery of reward, the rate of reward when the light is on (and the background is also present) is $\bar{\lambda}_l + \bar{\lambda}_b = n_l/t_l$, where n_l is the number of rewards delivered when the light is on, and t_l is the cumulative exposure to the light. Here, if there is no partial reinforcement ($S = 1$), then $n_l = n$ and $t_l = nT$ (see Figure 1A). Thus

$$\bar{\lambda}_l + \bar{\lambda}_b = \frac{n}{nT} = \frac{1}{T} \qquad\qquad \bar{\lambda}_b = \frac{1}{t_b} = \frac{1}{nI} \tag{2}$$

Notice that as the number of trials grows, and so more rewards are observed when the light is on, the estimated rate with the light is constant, whereas the background rate continually drops as $1/n$.

GG take the further important step of relating the rates λ_l and λ_b to the decision of the animals to start responding. GG suggest that acquisition should occur when the animals have strong evidence that the fractional increase in the reward rate while the light is on is greater than some threshold. Thus, acquisition should occur when there is sufficient evidence that:

$$\frac{\lambda_l + \lambda_b}{\lambda_b} > \beta \tag{3}$$

where β is the threshold (which should be greater than 1). As the actual rates are unobservable, inferred estimates of them must be used to decide whether or not the criterion has been met. RET uses mean rates for this purpose, asking when

$$\frac{\bar{\lambda}_l + \bar{\lambda}_b}{\bar{\lambda}_b} > \beta \tag{4}$$

Substituting the estimates given by Equation 2 gives $(1/T)/(1/nI) > \beta$, or equivalently:

$$n > \beta\left(\frac{I}{T}\right)^{-1} \tag{5}$$

which is evidently linear. This conforms to the empirical data in Figure 1B and Equation 1, for $\beta \approx 300$.

Under a partial reinforcement schedule, the number of trials it takes to observe n rewards becomes nS. However, the total time that the light is observed during these trials *and* the total time the background is observed by itself during these trials both go up by the same factor of S. Thus, partial reinforcement should have no effect on the number of rewards it takes for the acquisition criterion to be satisfied. As GG note, the irrelevance of S should be expected on the basis of Equation 1, since changing S does not change the effective I/T when measured as a function of reinforcements. For the remainder of the paper, we therefore no longer explicitly consider partial reinforcement.

RET suffers from two main problems, which motivated our search for an alternative. First, the value of $\beta = 300$ is inconsistent with data on the effects of presenting rewards when the background is present by itself (Jenkins, Barnes & Barrera, 1981). Second, the model is silent on why acquisition should be dramatically faster if the context is extinguished prior to autoshaping (Balsam & Schwartz, 1981; Balsam & Gibbon, 1988). The value $\beta = 300$ can also be ecologically questioned, since it suggests an inordinate statistical conservatism.

Firstly, under RET, rewards that are presented during the intertrial interval (when the light is off) are apportioned to the background, giving it a non-zero rate. Of course, this rate may nevertheless be lower than that for the light. In the case of figure 2A, for instance, $\lambda_l = 9\lambda_b$, and acquisition is found empirically to occur in 30 rewards, which is comparable to the speeds shown in Figure 1 (Jenkins, Barnes & Barrera, 1981). Under RET, acquisition can only occur at all if $(\lambda_l + \lambda_b)/\lambda_b > \beta$, and so this experiment provides an upper bound of $\beta \leq 9$. This bound is greatly at variance from the estimate $\beta = 300$ that comes from figure 1. To spell it out: either, if $\beta = 300$, then we would not expect acquisition at all in the Jenkins, Barnes & Barrera (1981) study; or, if $\beta = 9$, then the acquisition speeds shown in figure 1 should be thirty times faster (as shown in figure 2B). Even $\beta = 9$ is likely to be well above the actual threshold for response, since acquisition occurs relatively quickly for this I/T ratio, compared with its speed for other ratios.

Secondly, more evidence for this same conclusion comes from cases in which the context is extinguished prior to autoshaping. In most experiments in autoshaping, animals are given prior experience of reinforcements in the context alone (usually in the form of hopper training) to help familiarize them with the environment. The seemingly simple manipulation of extinguishing the context prior to autoshaping produces extremely rapid learning to the light (Balsam & Schwartz, 1981; Balsam & Gibbon, 1988). More generally, the speed with which responding to the light is acquired is strongly affected by the provision of rewards with the background alone, prior to autoshaping (Figure 3A; Balsam & Schwartz, 1981). Figure 3B shows the results of a study intended to examine this quantitatively. Balsam & Schwartz (1981) measured the acquisition speed during standard autoshaping as a function of the *number* of rewards provided in the context in the time before the light was introduced and autoshaping began (Figure 3A). As a control, the context was first extinguished to erase associations formed in hopper training before the rewards were provided in the context and without the light. Reconciling the data in Figure 3 and Figure 1 (*ie* Equation 1), it would seem that about 30 prior rewards must have been given in the context prior to conditioning to the light (for the studies in Figure 1), which is roughly consistent with the experimental procedures used (Gibbon et al, 1977; Gibbon & Balsam, 1981).

Equally important, and as pointed out by Gibbon and Balsam (1981), is that the rate at which these prior context rewards are presented seems to have little effect on the subsequent speed of acquisition to the light. Gibbon & Balsam (1981) considered acquisition times from a different set of experiments in which about 60 rewards were given in hopper training, prior to autoshaping, in each case at different rates. The differences in the rates of prior rewards had *no* significant effect on the speed of subsequent acquisition.

These data pose a tricky conundrum for RET for two reasons. First, Gibbon & Balsam (1981) interpret their data as implying that the rate associated with the context adapts quickly, so that the prior context rate does not affect the time it takes to acquire responding to the light. However, RET does not have this explanation open to it. Consider the case that the rates of delivery of reward before and after the light is introduced are the same. A natural mechanism in RET that allocates rewards between the light and the context would allocate all the rewards to the context, because no change in rate is consequent on the introduction of the light. Therefore, the animal should never acquire responding to the light. However, given other rates of delivery of reward to the light, RET would be forced to allocate rewards to the light, and so acquisition could happen. RET therefore predicts an essential dependence of acquisition on the rate at which the prior context rewards are delivered, contrary to Gibbon & Balsam (1981)'s data. A similar argument can be made that, under RET, there should be a dependence of acquisition times on the absolute difference between the reward rates before and after the light is introduced. None such is observed.

The second problem posed by the prior context rewards has to do with the strong dependence shown in figure 3B on the number that are provided. Gibbon & Balsam (1981)'s explanation that the speed of learning about the context is fast does not accommodate this aspect of the data. RET is similarly silent. Worse, however, under a statistical interpretation of RET, the dependence of acquisition rate on prior context rewards should be exactly the reverse of what is observed. To see this, consider the statistical effect of seeing more prior context rewards on the estimate of the rate of provision of rewards associated with the context. The more rewards that are observed, the less uncertain the subject should be about this rate (since the estimate of the rate will be based on more examples). Given a more certain prior rate of reward, a statistical test distinguishing this prior rate from a current rate of reward will be more powerful. Thus, the more readily RET should be able to decide that the rate has changed, if it does so. Therefore, if the rate of reward changes when the light is introduced, the subject should be able to decide this after fewer trials. Thus, it should more quickly decide to allocate the rewards to the light rather than the context, and so acquire responding more quickly. So, under this interpretation of RET, the more prior context rewards, the *faster* acquisition should be to the light. The data in figure 3B show exactly the opposite.

A further concern for RET comes from considering the certainty that the reward rate with the light is greater than that of the background at the time of acquisition. Consider a simple example with $T = 4$s and $I = 20$s, for which the animals take about 60 rewards to commence responding. Finding the reward during the 4s light rather than the 20s context is just like rolling a six-sided die and getting the answer '1' rather than '2-6' (since $T/(I + T) = 1/6$). Observing the consistent relation between the light and reward and deciding that the light is associated with an increased reward rate over the background is like throwing the die, observing a '1' each time, and deciding that the die is unfairly biased. It would likely take us a maximum of 5 or 6 rolls to draw the conclusion that the die is loaded (with a chance of error of 10^{-4}). Taking 60 die rolls leaves a miniscule chance of around 10^{-45} that the die is fair. It could be, of course, that animals are extremely conservative in autoshaping, compared to their much more reasonable inferential behavior in other paradigms. However, the data from the prior context manipulations (figure 3B) show that the animals can make detections at more reasonable speeds. Collectively these data suggest that RET's inferential model is incorrect, and inspire a consideration of alternatives.

3 The Competitive Model

The problems just outlined with GG form the constraints governing our new model. Furthermore, and this turns out to provide an important hint as to the construction of the model, we employed the extra constraint that pecking rates should follow the form of data such as figure 4A. This plot shows the development of responding to the light over the course of conditioning. GG's acquisition criterion is satisfied right at the beginning of learning (where the dotted line crosses the solid line); RET is mute on the approach of the rate of responding to its asymptote. Unfortunately, the latter phase of learning is not well explored experimentally, and is often obscured by the use of a liberal measure of behavioral response (see the Figure caption). For comparison, Figure 4B shows similar curves from the experiment of Balsam & Schwartz (1981) in which the number of prior rewards presented to a pre-extinguished context was controlled (to be 2 or 20).

In order to satisfy all these constraints, we take a different tack from RET. Our theory has two parts. The first part, described in section 3.1, is that each stimulus (the light and the context) is treated like an 'expert', learning independently about the world, and making an independent prediction of the rate of reward delivery. These predictions are based on a model which is a statistical generalization of standard conditioning theories like the Rescorla-Wagner (1972) rule, is designed to be consistent with scalar expectancy theory (SET; Gibbon, 1977), and is closely related to well-understood statistical and engineering methods for prediction. The second part of the theory, described in section 3.2, suggests that the predictions made by different stimuli should compete (Grossberg, 1982; Pearce and Hall, 1980) according to how *reliable* each stimulus is.

In our full model, learning is slow in standard autoshaping paradigms because the context acts as a more reliable expert, and, under the model, blocks the expression of the prediction made by the less established light. Extinguishing the context puts it and the light on a more equal footing, allowing for much faster expression of the learning associated with the light.

3.1 Expert Predictions

In this section, we specify how learning works for each stimulus or expert by considering a simplified case which assumes that each predicts the *total* rate that rewards are delivered while that stimulus is present. We start from the case that there is only one stimulus, namely just the context, and consider how it predicts the reward rate, why this prediction is uncertain, and how the uncertainty can satisfy the constraints suggested by SET.

The model (Kakade & Dayan, 2000; Dayan, Kakade & Montague, 2000) views the process of making predictions as one of reverse-engineering the way that the experimenter has programmed the experimental apparatus, using the observations of rewards provided. That is, at time t, the subjects consider there to be a parameter, $\lambda_c(t)$, under control of the experimenter, which governs the rate that rewards will actually be delivered to the animal in the context. For convenience, we suppress the time dependence where the dependence is clear. Here, the rate is just the probability per unit time of delivery of reward. This rate is a function of time, to reflect the possibility that the experimenter might change the reward contingencies over the course of the experiment. Rewards are presumed to be delivered statistically independently of each other.

The subject has to use the actual deliveries of rewards in order to figure out λ_c as best it can, and thereby predict the current relationship between the context and the rewards. Obviously, the subject's prediction, which we call $\hat{\lambda}_c$, can be uncertain. For instance, when the subject first encounters the context, it does not know whether it is to be given a low or high rate of reward. This uncertainty should reduce as it makes observations about the actual reward rate.

Appendix A provides a full treatment of the model. We consider just a didactic example, called a window model, which has similar properties, but is easier to understand. Unlike the full model, the window model uses the notion of a trial, and the estimate, $\hat{\lambda}_c$ is the observed rate of delivery of the last η rewards (the 'window'). That is $\hat{\lambda}_c = \eta/t_\eta$, where t_η is the length of time before t it took for the previous η rewards to be delivered. Note that this estimate will adapt to contingency changes, since it is not using any information from before t_η to construct its estimate. The estimate $\hat{\lambda}_c$ is based on η individual reward times. If the reward rate is actually fixed at $1/C$ during this time (where $C = I + T$ is the total length of a trial), then it is a standard result that the estimate $\hat{\lambda}_c$ is within a small factor of $1/C$, and the standard deviation of the estimate is within a small factor of $1/(C\sqrt{\eta})$. This means that the coefficient of variation of the estimate, which is the standard deviation of the estimate divided by its mean, is roughly $1/\sqrt{\eta}$, *independent* of the underlying rate λ_c.

The window model (and the full model of appendix A) show how the subject might construct an estimate $\hat{\lambda}_c$ of the reward rate, and that this estimate is uncertain to the tune of $1/\sqrt{\eta}$. This form of the uncertainty was inspired by SET, which notes that the uncertainty of estimates of time intervals has an asymptotically constant coefficient of variation. That is, no matter how many trials are measured, subjects do not get arbitrarily certain about time intervals, but rather have an uncertainty that satisfies an interval-independent relationship. The window model achieves the same result for the rates by measuring the time for a *fixed number* of rewards. The asymptotic uncertainty comes from the possibility that the experimenter might change the rate, invalidating the information from very old trials. Here, η determines how many trials are included in the total, and so should be set in line with the expected rate of change of λ_c. A small value of η will lead to quickly adapting estimates. The price to be paid for a small η is that each estimate is based on only a few rewards, and so is highly variable.

Since the light and the context are treated as making independent predictions, we will similarly have a prediction $\hat{\lambda}_l = 1/T$ with asymptotic standard deviation $\sigma_l = 1/(T\sqrt{\eta})$. What remains to be specified is how the conflicting estimates $\hat{\lambda}_c$ and $\hat{\lambda}_l$ are combined, since both provide predictions when the light is on.

3.2 Combining the Experts' Predictions

RET makes an assumption of additivity, *ie* that the estimates of reward rates of all stimuli present are added. By contrast, our model assumes instead that the stimuli *compete*. This idea is conventional in classical conditioning; however it is most commonly applied to how much *learning* should be accorded to stimuli (Mackintosh, 1975; Pearce and Hall, 1980) rather than how *predictions* from different stimuli should be combined (but see Grossberg, 1982).

When only the context is present, *ie* in the absence of competition, the prediction of the mean overall reward rate is $\hat{\lambda}_c^* = \hat{\lambda}_c$. However, when both the light and the context are present, we consider a model in which the joint prediction is a weighted average of the individual predictions rather than the sum. As an analogy, consider the task of estimating some fictitious value 'χ'. Expert 1 tells us the value of χ is χ_1, whereas expert 2 tells us the value is χ_2. In constructing an estimate of χ, we must average the two estimates based on how much we trust each expert. If we have equal trust in both experts, then our estimate of χ should just be the equally weighted average, $\frac{1}{2}\chi_1 + \frac{1}{2}\chi_2$. If we know expert 2 is highly unreliable, then our estimate should give little weight to expert 2 and should be rougly χ_1.

When both the light and the context are present, the combined prediction of reward, which we call $\hat{\lambda}_l^*$, is the weighted average

$$\hat{\lambda}_l^* = \pi_l \hat{\lambda}_l + (1 - \pi_l)\hat{\lambda}_c \tag{6}$$

where $0 \leq \pi_l \leq 1$ controls the degree of competition between light and context. We use an asterisk to denote the joint prediction made by all present stimuli. Again, we are suppressing the time dependence of the weighting π_l and the rates.

There are various ways that π_l might be determined (Kruschke, 1997; Dayan & Long, 1997). We (Dayan & Long, 1997; Dayan *et al*, 2000) have used the factorial experts model suggested by Jacobs, Jordan, & Barto (1991). In this, π_l is derived from underlying quantities called *reliabilities*, ρ_c and ρ_l for the context and light respectively, as

$$\pi_l = \frac{\rho_l}{\rho_l + \rho_c} \,. \tag{7}$$

The term reliability is used because of the statistical roots of the rule (Jacobs, 1995; Dayan & Long, 1997; Dayan *et al* 2000). One can interpret $1/\rho_l$ as the expected distance of the true rate associated with the light from the true overall rate – the more reliable the light as a predictor, the larger ρ_l, and the smaller the distance. Note how the prediction made by the context can block the prediction made by the light, provided that it is much more reliable ($\rho_c \gg \rho_l$). This is a *representational* form of blocking (Grossberg, 1982) rather than a learning form of blocking.

Unreliabilities and uncertainties are different, though related. Even if the subject was completely certain about $\hat{\lambda}_l$, it could accord the light little reliability as a predictor, on the basis of past experience, and so have a small value of ρ_l. To be strictly accurate, the uncertainties in the estimates $\hat{\lambda}_c$ and $\hat{\lambda}_l$ should decrease the terms ρ_c and ρ_l in equation 7, but this is typically only a small correction. Ideally, we would be able to specify a statistically normative model governing the setting of the reliabilities. Unfortunately, as will be apparent in the next section, there is presently little evidence about the constraints on the model (unlike, for instance, the evidence from SET about the uncertainties). Therefore, we will content ourselves with a phenomenological model for them.

4 Modeling Acquisition and Extinction

We can now combine the two parts of the model to account for the data on acquisition and extinction. Crudely, the predictions associated with the context and the light both adapt quickly, within $\eta = 25$ rewards. There is thus no blocking in the learning of the prediction of the light because of the prediction made by the context. However, the expression of the prediction associated with the light happens slowly, since the context, particularly in the face of hopper training, is treated as being more reliable. We do not present a normative account of how the reliabilities change, due to a lack of data on the slower phase of learning. Rather we show that the model is capable of fitting the data with an assumption of how the reliabilities do change. During extinction, the reliability of the light is almost constant, so the speed is determined just by η.

4.1 Acquisition

A fully normative model would come from a statistically correct account of how the reliabilities should change over time. This, in turn, would come from a statistical model of the expectations the animal has of how the predictabilities of stimuli and rewards change in the world. The best data for this comes from the slow phases of learning in figure 4, since it is during this period that the light is becoming treated as more reliable. Unfortunately, the slow phase is widely ignored in experiments. Further, as GG point out, the existing data presented is averaged over subjects, thus obscuring the behavior of individual subjects. We are therefore forced to make an assumption to fit the acquisition data. We state this assumption in terms of the combination weights $\pi_l(n)$ rather the reliabilities themselves Here, n indexes the time the nth reward is presented, and, for simplicity, $\pi_l(n)$ is assumed constant between rewards.

Rather than using something purely arbitrary, we assume that the animal's response rate during the slow, post-acquisition, phase of learning follows the estimated reward rate. As seen in figure 4, the response rate is sigmoidal, and so is nicely modeled by a tanh function. Working backwards, for this to be the form of the estimated reward rate, the relatively responsibility $\pi_l(n)$ should follow

$$\pi_l(n) = \tanh \pi_0 n \tag{8}$$

where π_0 is a constant that is independent of I/T (which is essential for the model to fit the data). Figure 5 compares the rate of key pecking in the model with the data from Figure 4A. Slow acquisition to the light comes from slow changes in the importance accorded to the long established predictions made by the light.

A decision criterion for a subject turns its estimates of the rates of reward into a time at which they start responding reliably. Following GG, we assume that responding commences when they expect a sufficiently higher response rate with than without the light, that is, when they have good reason to believe that

$$\lambda_l^* > \beta \lambda_c^* \tag{9}$$

From section 3.1, the estimated means of these rates are

$$\hat{\lambda}_c^* = \frac{1}{C} \quad , \quad \hat{\lambda}_l^* = \frac{1}{C} + \pi_l(n)\left(\frac{1}{T} - \frac{1}{C}\right) \tag{10}$$

Using these in the decision criterion (which is a good approximation), the threshold value becomes

$$n > \left(\frac{\beta - 1}{\pi_0}\right) \left(\frac{I}{T}\right)^{-1} \tag{11}$$

(since $\pi_l(n) \approx \pi_0 n$ for early n) which gives the correct linear dependency on I/T. Note that the constant of proportionality is $(\beta - 1)/\pi_0$ rather than the factor of β predicted by RET (Equation 5). Comparing Equations 1 and 11, we see that $(\beta - 1)/\pi_0 = 300$. For π_0 obtained by fitting the post-acquisition behavioral response curve (Figure 5A), this gives a value of $\beta \approx 2$.

This is a more reasonable value of β that is not inconsistent with the data on the provision of rewards during the context (Jenkins *et al,* 1981), and implies that detection will occur for almost all reward rates associated with the light that are larger than those for the context.

The data on pre-exposure of the context show that the number of rewards provided before the light is shown exerts a strong effect on the speed of acquisition. In the model, these prior rewards serve to increase the reliability of the context in the early stages of conditioning. From Equation 7, since $\rho_l(n)$ is small, the effect of this on the weight $\pi_l(n)$ of the light is to change the *slope* π_0. Figure 6A shows the effect on the predicted behavioral response of varying π_0. The center dashed line is the same as in Figure 5. The numbers labeling the curves are the values of π_0 as multiples of the value of π_0 for the center curve. This figure shows that by varying the initial weight by a multiplicative factor of between 0.3 and 3, the acquisition speeds (judged at the criterion line shown) due to between 1200 and 0 prior context rewards can be obtained, making the model consistent with the data in Figure 3.

Prior context manipulations also strongly affect the post-acquisition response curves, as shown in Figure 4B. Figure 6A shows the strong effects on the long term response curves of varying π_0. Figure 6B fits the overall response curves of Figure 4B (using $\pi_0 = 0.0023$ and $\pi_0 = 0.0085$). Note that the lower curve looks substantially far from its asymptote. These different values of π_0 are assumed to come from manipulations to the reliability of the context, and are affected by extinguishing the context and providing precisely controlled numbers of rewards in the context. The rate at which the prior context rewards are provided has little effect (Gibbon & Balsam, 1981), since the speed of adaptation to the new rate of the prediction associated with the context is fast (within around $\eta = 25$ rewards), compared with the speed of change of the reliabilities.

4.2 Extinction

Figure 7 shows experimental data indicating that the number of reinforcements that must be omitted, $\overline{n}$, to reach an extinction criterion that the rate in responding to the light should halve, satisfies

$$\overline{n} \approx 50 \tag{12}$$

In striking contrast to acquisition, the I/T ratio has no effect on extinction.

Since our model of acquisition explicitly allows contingencies to change over time, it lends itself naturally to extinction. In the model, the prediction of the *current* reward rate with the light constantly decreases when the light is no longer reinforced. Consider associating a decline to 50% of the pre-extinction rate of responding as occurring when the current rate estimate of the animal has decreased to of the order of 50% of its pre-extinction estimate. We make the crucial assumption that the reliability of the light does not change significantly over the early phase of extinction.

Consider the simple window model in which rates are assessed by calculating the total time that elapsed for the last η rewards (extinction in the full model is treated in appendix B). According to this measure, the pre-extinction reward rate is $\hat{\lambda}_l^{\text{pre}} = \frac{1}{T}$. After $\overline{n}$ omitted rewards during extinction (*ie* at time $\overline{n}T$ after the beginning of extinction), the post-extinction reward rate is $\hat{\lambda}_l(\overline{n}) = \eta/(\eta + \overline{n})T$, since the last η rewards occurred in time $\eta T + \overline{n}T$. The ratio between $\hat{\lambda}_l^{\text{pre}}$ and $\hat{\lambda}_l(\overline{n})$ is $1/2$ when

$$\overline{n} = \eta \tag{13}$$

which shows that the number of omitted rewards until extinction is approximately the number of remembered rewards η. This is clearly independent of I/T. Note that measuring the window size by rewards, itself chosen in the light of SET, is crucial to obtain this correct dependency.

Equations 12 and 13 can be combined to provide an estimate based on extinction of $\eta \approx 50$ that can be compared with the estimate based on acquisition. This provides an independent check on the model. This value is a little higher than that implied by the data on acquisition. One potential source of error is the assumption that there is a direct relationship between the behavioral response and the estimated association between light and reward. If the 50% decline in response occurs when the current rate is about 30% of its pre-extinction rate, then we obtain $\eta \approx 25$, which is just the same as that for acquisition. The general dependence of this fractional drop of the estimated rate is discussed in appendix B.

With $\eta \approx 25$, the same set of parameters are used to model both acquisition and extinction. However, for acquisition, the crucial parameter is π_0, which reflects the speed at which the reliabilities changes, whereas for extinction, the crucial parameter is η, which reflects the speed at which the estimated contingency between the light and reward could change.

5 Discussion

The speeds with which animals acquire and extinguish conditioned responses in autoshaping conform to a set of simple quantitative relationships. Normative models suggest that such relationships arise when animals make *optimal* inferences based on their underlying statistical assumptions. Different statistical assumptions (which amount to different ecological expectations) lead to different normative models, and different predictions about the speed of acquisition and extinction.

Gallistel and Gibbon (2000) were the first to suggest a normative account for the autoshaping data. Unfortunately, although their model correctly captures the nature of the dependency of the speed of learning on various parameters, its quantitative predictions on the speed of acquisition and extinction are inconsistent with the data. Further, the model has little to say about longer term behavior during acquisition and extinction or about the effects of extinguishing the context prior to the initiation of autoshaping.

We have suggested an alternative normative model to account for both the data underlying GG and the results of other experiments. Although our model's focus is on acquisition and extinction, it is governed by a rich set of quantitative constraints. First, since animals can be ideal detectors of rates in some circumstances (*eg* Gallistel, Mark, King, & Latham, 2001), we required an account under which their acquisition of responding could be given a rational statistical basis. In this sense, the rate of responding during learning should be based on an optimal evaluation of the contingencies given the observations so far provided. Second, as in GG, the number of reinforcements to acquisition should be governed by the relationship $n \approx 300(\frac{I}{T})^{-1}$, as shown in Figure 1B. This also implies that S, the partial reinforcement schedule, should be irrelevant. Third, pecking rates after the acquisition criterion is satisfied should rationally follow the form of Figure 4. However, as insufficient data exist on this phase of learning, our model makes specific assumptions to capture this constraint — and thus falls short of providing a completely normative account. Fourth, the overall learning speed should be strongly affected by the *number* of prior context rewards (Figure 2B), but not by the *rate* at which they are presented. That is, regardless of the rate it predicts, the context, as an established predictor, should be able substantially to *block* a less established predictor. Fifth, the rate estimates must not become arbitrarily accurate, and their asymptotic uncertainty should be consistent with SET.

Our model is built on a set of statistical assumptions which take explicit account of two central concerns for estimation, *uncertainty* and *unreliability.* Uncertainty, also a facet of scalar expectancy theory, comes because information from observations of reward is traded off against the possibility that the reward rates might change. Uncertainty governs the observed rate of extinction. Unreliability, a higher order property of a stimulus, comes as part of an adaptive filtering strategy, and changes only slowly. The most unsatisfying aspect of the model is the lack of a normative account of how unreliabilities should change – this is largely due to a lack of experimental data on the slow phase of responding.

The model of unreliability derives from Dayan & Long (1997), who, following Grossberg (1982), used it to account for data on a set of paradigms, including downwards unblocking (*eg* Holland, 1988). Dayan & Long's (1997) model does not conform to the quantitative timing relationships studied here. Kruschke (1997) suggested an alternative competitive account derived from a different statistical model called the mixture of Gaussians model (Jacobs, Jordan, Nowlan & Hinton, 1991). Models such as ours and Kruschke's (1997), in which stimuli are perfect competitors for each other, and their predictions are combined using a weighted *average*, lie at one end of a spectrum and capture these blocking effects. At the other end of the spectrum, lies the Rescorla-Wagner rule (and also the rate additivity assumption of RET), in which stimuli are perfect cooperators and their predictions are simply *summed*. Additive models cannot simply account for paradigms such as downwards unblocking (Holland, 1988). However, there is also experimental evidence in favor of additive combination, particularly in paradigms involving conditioned inhibition (see Rescorla, 1988) or those involving signalled background reinforcers (Durlach, 1983), which our competitive models cannot simply account for. Understanding the rules governing competitive and additive combination is a major task for future theoretical work.

The model is also incomplete. For instance, data from Balsam & Schwartz (1981) suggest the possibility of a sustained difference in maintenance response rates as a function of the amount of pretraining. Our model leaves such a possibility open depending on the asymptotic value of the weight, π_l, of the light's prediction. Equation 8 assumes that the asymptotic value of the combination weight is one, which implicitly assumes that the context is treated as being asymptotically much less reliable than the light (and so the expression of its prediction is completely blocked). If this is not true, then sustained differences in responding might occur as the combination weight's asymptote will be lower. There are three further complications in interpreting the long-run, maintenance, keypeck rates. First, Figure 5 and Figure 6B show that the number of trials before asymptotic response behavior is apparent may be extremely long, outside the realm of many experiments. Second, data from Gibbon *et al* (1977) argue that maintenance keypeck rates depend on T more strongly than on I. This may also play a role in the results of some autoshaping experiments (*eg* Holland, 2000) in which the linear dependence of acquisition times to I/T is not valid across as wide a range as is evidence in figure 1B;C. Third, Pearce & Collins (1987); Swan & Pearce (1987) suggest that these rates also reflect an orienting response to the light whose strength depends on the accuracy with which its consequences can be predicted. This last effect is of significance primarily in the cases of partial reinforcement (for which $S > 1$). Also, effects of changing the magnitude of reward (which can take various forms; see, for example, Balsam & Payne, 1979; Allan & Ziegler, 1994; Ploog & Ziegler, 1996) are not modeled.

Finally, we have so far not considered the strong evidence that the animals can perform interval timing, *ie* predicting the time after the illumination of the light that the reward will be delivered. This capacity evident in the average pattern of responding, as well as from other experiments such as the peak procedure (see Gallistel & Gibbon, 2000 for a discussion). This implies that the animals may not be making predictions about a single reward rate during the light, but rather multiple reward rates during separate portions of the light.

Other experiments could test the assumptions of the model. For instance, one expectation is that the asymptotic prediction variance, which is closely tied to the learning rate, should depend on the expected speed of change in the environment. It would be interesting to present animals with a series of autoshaping tasks with different values of I/T, changing between them either quickly or slowly. We would predict that the animals should show fast and slow adaptation to the rates accordingly. There is some evidence for this sort of 'meta-learning' in other cases (*eg* Krebs, Kacelnik & Taylor, 1978).

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6 Appendices

A The Kalman Filter Model

In our model, the subject attempts to estimate the parameters governing the experimental situation based on observations. Although the most natural parameters are the rates $\lambda_c(t)$ and $\lambda_l(t)$ themselves, we consider a model couched in terms of the inverse rates $s_l(t) = 1/\lambda_l(t)$ and $s_c(t) = 1/\lambda_c(t)$, which are the times between rewards. We have confirmed with simulations that this does not affect our conclusions. Since the light and context act independently, we consider just the context, and drop the subscript. Because of the scalar property enshrined in SET, we assume that we measure estimation time in terms of numbers of rewards rather than clock time, and so write $s(n)$ rather than $s(t)$.

To specify the model, we have to indicate how the current value of the inverse rate $s(n)$ leads to an observed interval $o(n+1)$ between rewards (this is called the output model), and then how the inverse rate can change (the dynamic model). We make simple Gaussian assumptions

$$\text{the output model} \qquad o(n+1) \sim \mathcal{G}(s(n), s(n)^2) \tag{14}$$

$$\text{the dynamic model} \qquad s(n+1) = s(n) + \epsilon(n) \tag{15}$$

$$\text{the fluctuation model} \qquad \epsilon(n) \sim \mathcal{G}(0, (\sigma s(n))^2) \tag{16}$$

The scalar property governs the form of the output model (equation 14) and also the variance of the fluctuations $\epsilon(n)$ in the dynamics model. Here, $\sigma < 1$ is a unitless parameter that sets the scale for how fast the rates can change. Strictly speaking, $s(n+1)$ is truncated at 0, so that the inverse rate is prevented from being negative, but this is in any case unlikely.

If the variances in Equations 14 and 16 were constant, then a completely standard Kalman filter (Anderson & Moore, 1979) would exactly specify the probability distribution of the current estimate of $s(n)$, in light of the above equations and the observed rewards. We make the extra approximation of using the standard Kalman filter, but estimating the variances using just the means, $\hat{s}(n)$, and not worrying about the recursive effects of uncertainty in $\hat{s}(n)$ on the variance. Since the distribution for $s(n)$ is Gaussian, the Kalman filter only specifies update rules for the mean $\hat{s}(n)$ and variance $v(n)$ of the estimate of $s(n)$.

$$\hat{s}(n+1) = \hat{s}(n) + \alpha(n)(o(n) - \hat{s}(n)) \tag{17}$$

$$v(n+1) = (v(n) + (\sigma\hat{s}(n))^2)(1 - \alpha(n)) \tag{18}$$

Notice that the update rule for $\hat{s}(n)$ is a delta rule, just like a Rescorla-Wagner (1972) rule with $\alpha(n)$ acting as the learning rate parameter. This learning rate is given by:

$$\alpha(n) = \frac{\sigma^2 + v(n)/\hat{s}(n)^2}{\sigma^2 + 1 + v(n)/\hat{s}(n)^2} \tag{19}$$

The dependence of the learning rate on the output and fluctuation variances is necessary to match the speed with which the world is expected to change and the degree of certainty in the current estimate.

In this approximate model, the asymptotic variance is a constant multiple of the mean. This satisfies the SET constraint of an asymptotically constant CV (as can be verified from Equation 18). In particular, the choice of

$$\sigma^2 = \frac{1}{\eta(\eta - 1)} \tag{20}$$

gives a terminal CV of $1/\sqrt{\eta}$. This gives an asymptotic learning rate of $\alpha = \frac{1}{\eta}$, as can be easily verified from Equation 19.

After observing n rewards, at time $t = nC$, the posterior distributions for the inverse rates become

$$p\,(s_c(n)|\text{data}) \sim \mathcal{G}(C, v_c(n)) \qquad p\,(s_l(n)|\text{data}) \sim \mathcal{G}(T, v_l(n)) \tag{21}$$

and, in about η rewards, $\sqrt{v_c(n)} \to C/\sqrt{\eta}$ and $\sqrt{v_l(n)} \to T/\sqrt{\eta}$. This satisfies the constraint suggested by SET, and also allows rates to adapt quickly under appropriate circumstances.

B Extinction

The approximate model in appendix A closely matches the full model in the text, but it only provides estimates of the time between rewards at the times that rewards are themselves delivered. In extinction, we are interested in the full model's estimate of the reward rate at times when rewards are not presented. We now specify an extension of this approximation that estimates the rate in the period between rewards, and which also closely matches the full model (again, as verified by simulations).

As discussed in the text, we assume that the light's reliability changes insignificantly over the early phase of extinction, and so the overall predicted rate of reward during extinction whilst the light is present continues to be given by the light's prediction alone.

Like GG, we measure time in terms of the number of omitted rewards. We treat an observation of $\overline{n}$ of these in time $\overline{n}T$ as an observation of a current reward rate of $1/\overline{n}T$, and use this observation, in conjunction with the previous estimate from the last actual delivery (of $\hat{t}_l^{\text{pre}}$, and the previous asymptotic learning rate of $1/\eta$ according to equation 18):

$$\hat{t}_l(\overline{n}) = \hat{t}_l^{\text{pre}} + \frac{1}{\eta}(\overline{n}T - \hat{t}_l^{\text{pre}}) \tag{22}$$

where $\hat{t}_l^{\text{pre}}$ is $1/\hat{\lambda}_l^{\text{pre}}$, and $1/\eta$ is the asymptotic learning rate. From equation 22, an approximate estimate of the mean rate $(1/\hat{t}_l(\overline{n}))$ is:

$$\hat{\lambda}_l(\overline{n}) = \left(\frac{\eta}{\eta + \overline{n} - 1}\right)\frac{1}{T} \tag{23}$$

Notice this also agrees with the estimate from the didactic 'window' model described in the text.

As argued in the text, we model GG's extinction criterion as occurring when:

$$\hat{\lambda}_l(\overline{n}) < \beta_e \hat{\lambda}_l^{\text{pre}} \tag{24}$$

where β_e is a threshold less than one (which represents the fraction of the pre-extinction rate the current estimate must fall below to justify a 50% decline in the response rate). Of course, this is *not* a statistical decision criterion for the animal, but instead it comes from measuring the extinction speed using a comparison of the current response rate to the pre-extinction response rate.

Solving this for $\overline{n}$ using equation 23, gives

$$\overline{n} > \eta(\frac{1}{\beta_e} - 1) + 1 \tag{25}$$

For $\beta_e = 1/3$ and $\eta = 25$, this makes the estimate of $\overline{n} \approx 50$, as shown in Figure 7.

Figure Captions

Figure 1: Autoshaping. A) Experimental paradigm. Top: the light is presented for T seconds every C seconds and is always followed by the delivery of food (filled circle). Bottom: the food is delivered with probability $1/S = 1/2$ per trial. In some cases I is stochastic, with the appropriate mean. B) Log-log plot of the number of reinforcements to a given acquisition criterion versus the I/T ratio for $S = 1$. The data are median acquisition times from 12 different laboratories. A linear fit to $\log I/T$ is shown. C) Log-log acquisition curves for various C/T ratios and S values. The main graph shows *trials versus S*; the inset shows *reinforcements versus S*. Adapted from Gallistel & Gibbon (2000).

Figure 2: A) Figure not drawn to scale. Rewards given in the intertrial interval at constant rate of $1/75$ sec, while the rate with light is $1/8$ sec. Acquisition occurs in about 30 rewards for this case (Jenkins, Barnes, & Barrera, 1981). B) As discussed in the text, β must satisfy $\beta \leq 10$ for acquisition to occur in A. The solid line shows the predicted acquisition speed for $\beta = 10$ for various I/T values, and, for comparison, the crosses show the actual acquisition speeds as in figure 1B. Acquisition is predicted to be 30 times too fast.

Figure 3: Context Manipulations A) Following extinction of the context (not shown), a fixed number of rewards is given in its presence, and without the CS. Subsequent autoshaping pairs the rewards with the light. B) The effects of such prior context reinforcements on subsequent acquisition speed. The data are taken from two experiments, both with $I/T = 6$. (The data are from Balsam & Schwartz (1981), except for 0 and 1200 prior context rewards, which are from Balsam & Gibbon (1988).)

Figure 4: Acquisition of keypecking showing response rate *versus* reinforcements. A) The standard acquisition criterion is satisfied when the animal responds on three out of four consecutive trials, when the response curve crosses the acquisition criterion line shown. Data

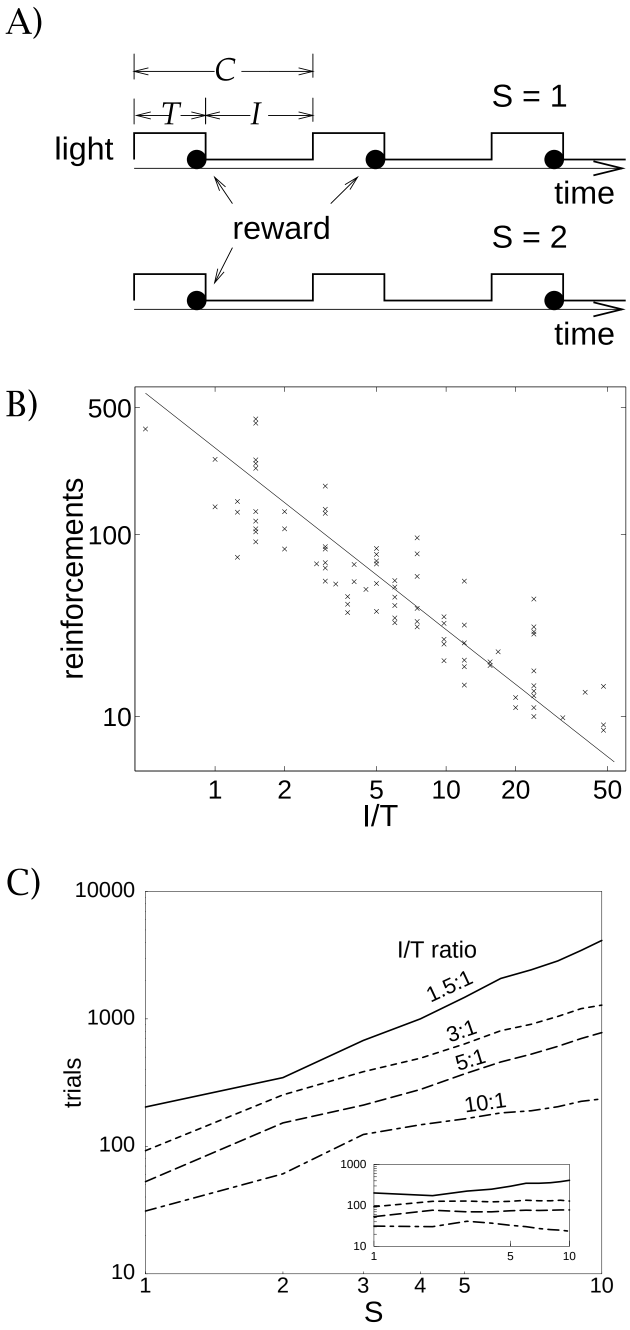
are averaged from 11 animals, so the sharper transition from no conditioned response to the initial responding is smoothed. Most often these data are obscured by using a permissive measure of behavioral response such as the percent of trials within a session in which at least one response occurs. The percent of trials with at least one response often saturates, close to 100%, relatively quickly after the standard acquisition criterion is met. As seen in the Figure, the animals usually continue to increase their response rates over a longer time scale. Adapted from Gamzu & Williams (1973). B) Longer term behavioral response for two different pre-training cases. The top curve is for 2 prior context rewards; the bottom curve is for 20 prior context rewards. Pretraining not only affects the short time to acquisition, but also the slower phase of learning. Data from Balsam & Schwartz (1981).

Figure 5: Fit to the behavioral response curve (figure 4A), using Equation 8 with the constant $\pi_0 = 0.004$. Here, the response to the light is modeled as being proportional to the increased reward rate with the light, i.e. the difference between the estimated reward rate with the light, $\hat{\lambda}_l^*(n)$ and the estimated reward rate with the context $\hat{\lambda}_c^*(n)$.

Figure 6: Satisfaction of the Constraints. A) Possible acquisition curves showing the estimated reward rate with the light, $\hat{\lambda}_l^*(n)$, *versus* n. Again, I is the length of the intertrial interval, T is the time during the trial for which the conditioned stimulus is presented, and $C = I + T$. The dashed curve is the same as in figure 5. The parameters displayed are values for the constant π_0 in equation 8 in multiples of π_0 for the center curve. As only π_0 is varied and not I or T, the speed of acquisition can be measured when the curve crosses the acquisition criterion line shown. The $\longleftrightarrow$ on the criterion line denotes the range of acquisition speeds (between 15 to 120 reinforcements) shown in figure 3, as due to between 0 and 1200 prior context rewards. B) The post-acquisition response curves of Figure 2B are fit just as in Figure 5. Here, $\pi_0 = 0.0023$ for the top curve and $\pi_0 = 0.0085$ for the bottom curve.

Figure 7: Log-log extinction curves for various I/T ratios and values of S. The main graph

shows *trials to extinction* versus S (different curves are for different I/T ratios); the inset shows *omitted reinforcements versus* S. This shows that the number of omitted reinforcements until the extinction criterion is approximately 50. I/T ratios go from 1.5 : 1 to 25 : 1. Adapted from Gallistel & Gibbon (2000).



A)
C
T
I
S = 1
light
time
reward
S = 2
time
B)
500
100
10
reinforcements
1
2
5
10
20
50
I/T
C)
10000
1000
100
10
trials
I/T ratio
1.5:1
3:1
5:1
10:1
1
2
3
4
5
10
S

Figure 1:

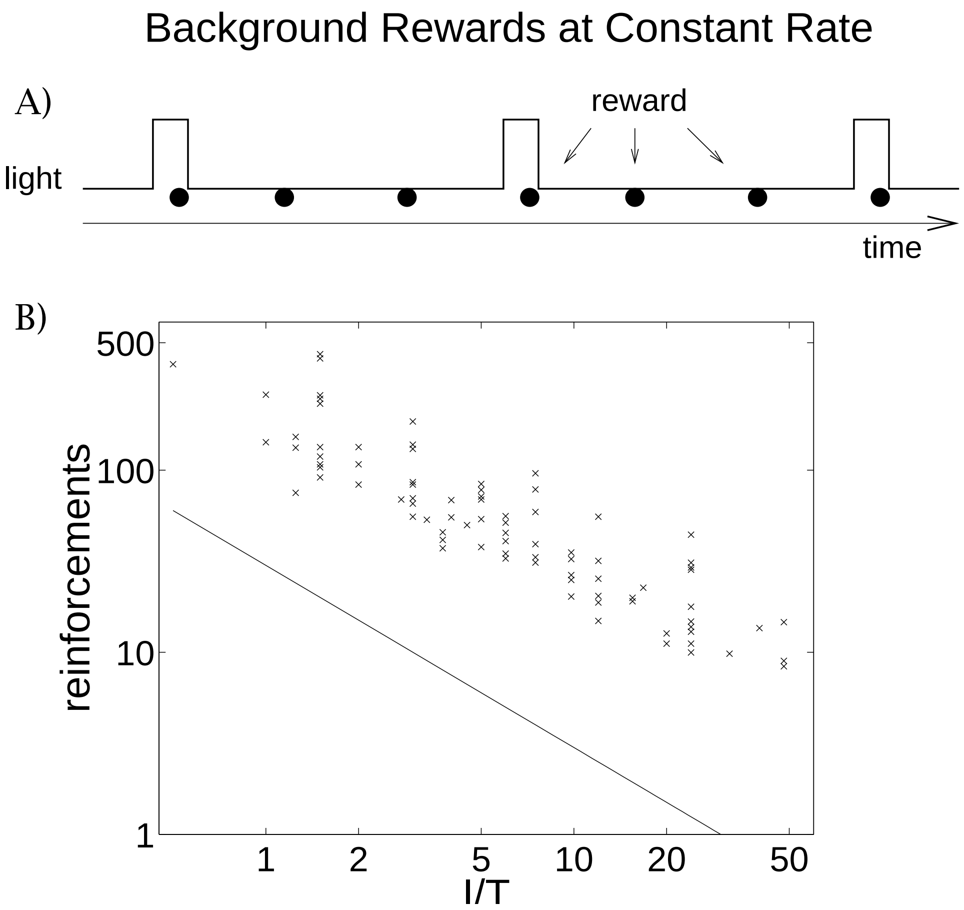
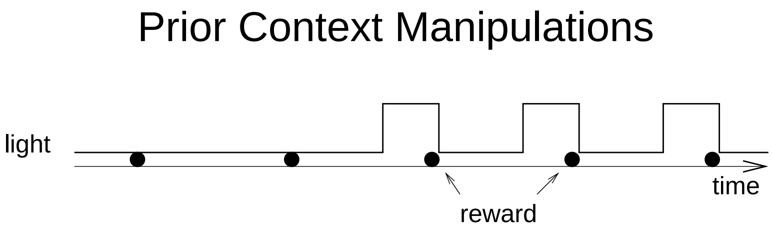

Background Rewards at Constant Rate
A)
reward
light
time
B)
500
100
10
1
reinforcements
1
2
5
10
20
50
I/T

Figure 2:

A)


Prior Context Manipulations
light
time
reward

B)

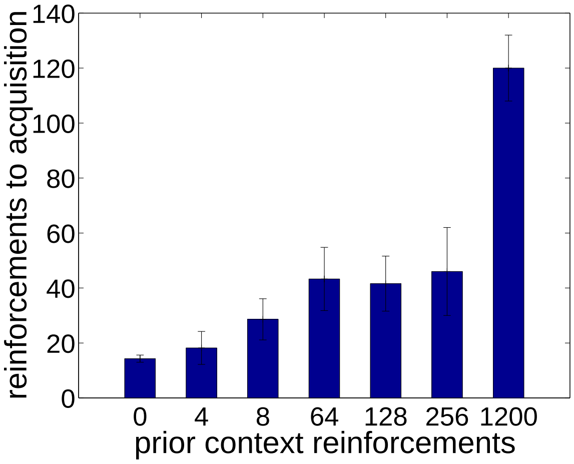
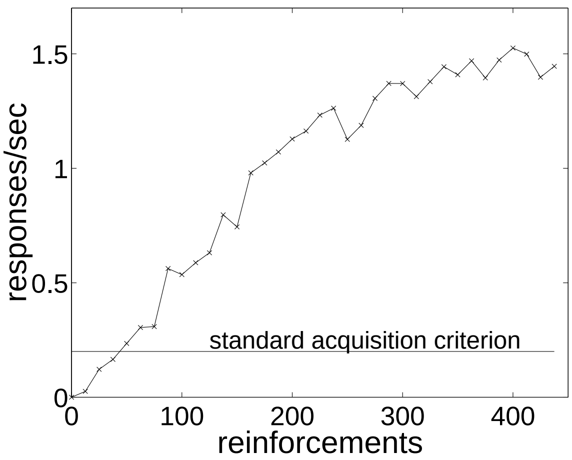

reinforcements to acquisition
0
20
40
60
80
100
120
140
0
4
8
64
128
256
1200
prior context reinforcements

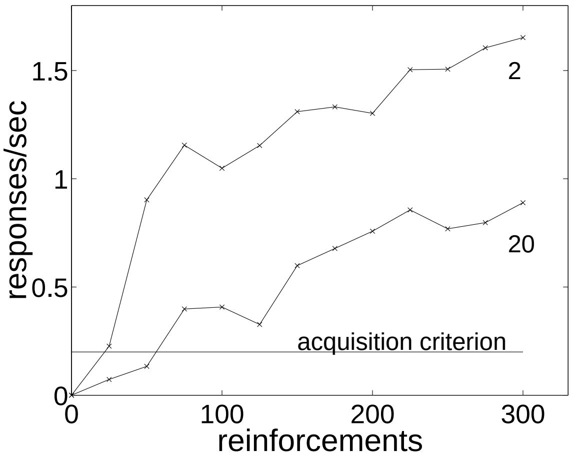
Figure 3:

A



1.5
1
0.5
0
responses/sec
standard acquisition criterion
0
100
200
300
400
reinforcements

B



1.5
1
0.5
0
responses/sec
2
20
acquisition criterion
0
100
200
300
reinforcements

Figure 4:

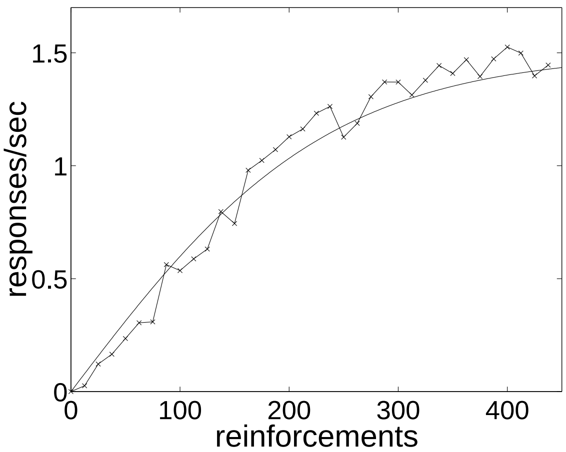
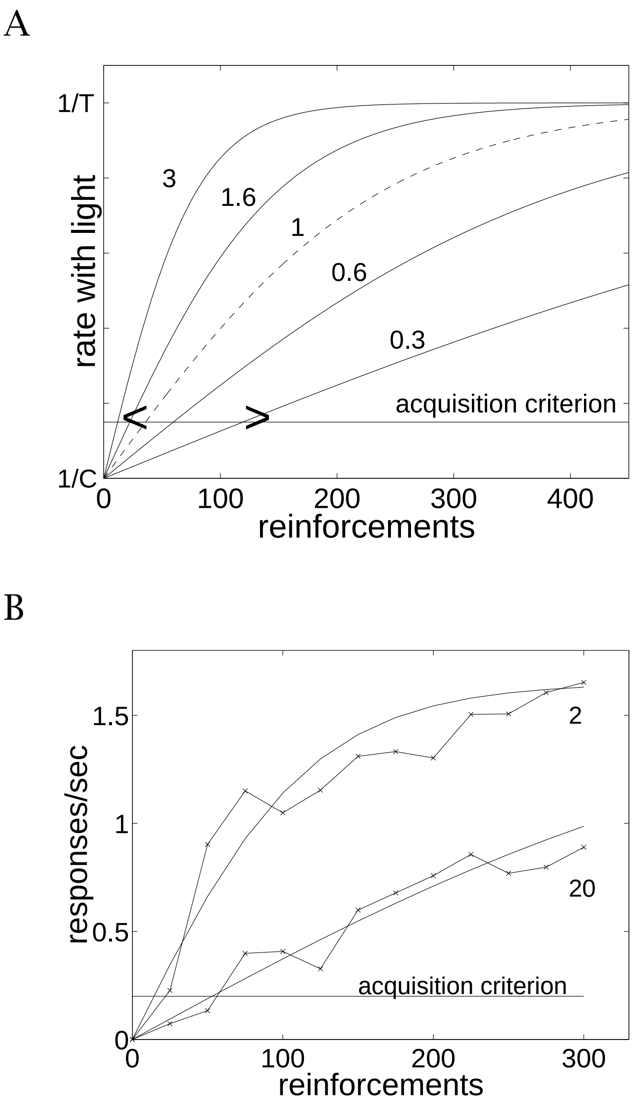


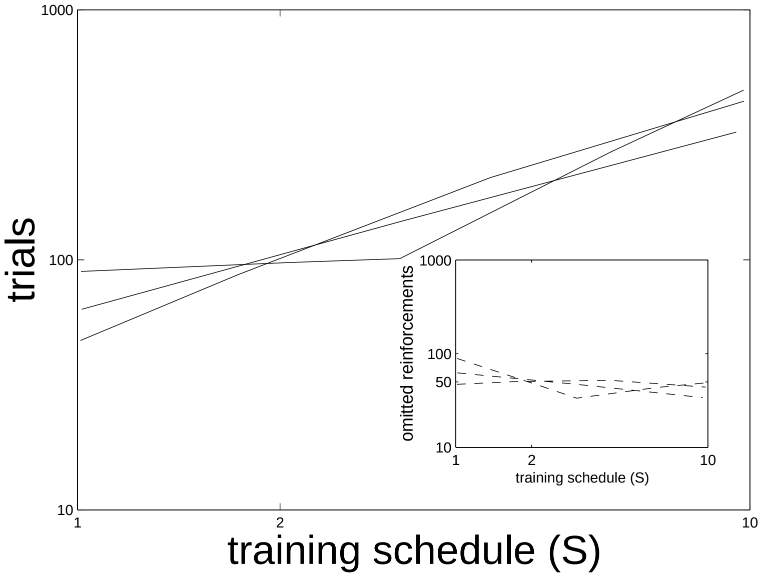
Figure 5:

A



1/T
3
1.6
1
0.6
0.3
acquisition criterion
1/C
0
100
200
300
400
rate with light
reinforcements
B
responses/sec
1.5
1
0.5
0
2
20
acquisition criterion
0
100
200
300
reinforcements

Figure 6:



trials
training schedule (S)
1000
100
10
1
2
10
omitted reinforcements
1000
100
50
10
1
2
10
training schedule (S)

Figure 7: