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# Pavlovian conditioning from a foraging perspective

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## Abstract

Principles in foraging and standard associative learning theories motivate a model for Pavlovian conditioning. The model tracks distal and proximal scales of expected reward probabilities plus the strength of signal-reward association. A combined reward probability is developed by combining the distal and proximal estimates through their uncertainties. Possible neural structure equivalents to the model variables are discussed. Model flexibility is demonstrated with data on the partial reinforcement extinction effect, a phenomenon difficult to explain with learning models.

**Keywords:** Mathematical model; Pavlovian conditioning; associative learning; foraging theory; partial reinforcement extinction effect, neural structures.

## Foraging and Associative Learning

Pavlovian conditioning (PC), or associative learning, is one of the most well studied psychological processes and has an array of associated phenomena. The two main processes, acquisition of a behavior by pairing a signal and reward in trials and extinction of the behavior by removing the reward during the trials, can be explained by a number of models, the most common being the delta model where learning is guided by the error, i.e. delta, between the expected and received reward per trial (Rescorla & Wagner, 1972). However, the basic delta model cannot explain other widely known phenomena, including spontaneous recovery of behavior when signaling trials are conducted after extinguishing the behavior and the partial reinforcement extinction effect (PREE) where intermittent rewards during acquisition trials increase the resistance to extinguishing behavior and strengthen the response during spontaneous recovery trials. In particular, the PREE challenges associative models of PC, since lower reward expectations for partial compared to continuous reinforcement would appear in principle to produce faster extinction. One theory for PREE involve the rate of reinforcement, such the ratio of the current cumulative signal duration since the last reward to the average signal duration between rewards (Gallistel & Gibbon, 2000). However, this result is not supported experimentally (Haselgrove et al., 2004). An alternative verbal model proposed by Pearce et al. (1997) assumed that

unrewarded trials during partial reinforcement schedules create a different context where the unrewarded trials signal rewarded trials. We develop a model that readily explains PC phenomenon in what we believe is a robust manner. Our model builds on PC and foraging theories and the neuroscience of memory and decision-making.

Animals in natural and laboratory environments meld their past and current experiences in making decisions; it is often assumed that the laws and processes in both environments are similar if not identical. In foraging, animals choose between staying in the current patch and moving to another. Deciding when to give up on a patch depends on the expected reward rate of the current patch relative to the expected reward rate on another patch discounted for the interpatch travel time (Charnov, 1976). In PC the response rate reflects expectations within the single environment as dependent on learning and unlearning of signal-reward associations (Bouton, 1993). Notably, in both frameworks, responses are based on comparisons of distal and proximal information. Distal information in PC is the memory of the previous signal-reward patterns, while in foraging distal information is the memory of the average habitat reward rate. Proximal information in PC reflects the most recent reward outcomes, while in foraging it reflects the expected foraging rate in the current patch. In both frameworks, expected reward for the next trial is computed by a delta rule, which is an exponentially weighted moving average (EWMA) that adds a percentage of the most recent outcome to a percentage of the previous expectation.

The two frameworks diverge in how non-reward events and extinction are treated. PC models commonly consider acquisition-extinction patterns in terms of distinct learning streams. A stream developed during the acquisition phase of the experiment characterizes signal-reward expectations, and a second stream developed during the extinction phase characterizes a signal-no reward expectation. Extinction learning inhibits the original acquisition learning (Bouton, 1993). However, when animals are retested after some interval of time the extinction learning is forgotten and spontaneous recovery of the original learning appears (Sissons & Miller, 2009). In foraging models, the learning streams do not inhibit each other nor are they forgotten.

Expected probabilities of rewards are tracked for both the current patch, i.e. the proximate patch, and the habitat, i.e. the distal patch. With parallel information streams, the animal does not need to distinguish whether information belongs in the acquisition or the extinction learning stream, an issue in PREE experiments where signals without rewards occur during the acquisition phase. Rather, the animal is constantly adapting to an always changing environment.

Patch foraging models naturally involve multiple temporal scales because information on the proximal patch is always more recent than information on distal patches. To capture these temporal differences, models have expressed distal and proximal learning with slow and fast learning rates respectively (Anderson, 2002; Moorter et al., 2009). Mixed learning rates are also used in the primary value learned value (PVLV) model (O'Reilly et al., 2007), that seeks a mapping to dopaminergic neuron dynamics during reinforcement learning.

Retaining reward probabilities across different temporal and spatial scales requires memory systems, and here neuroscience provides information on their nature. McClelland et al. (1995) postulated memories are created and stored in a two-stage process involving short- and long-term processes. First, events are stored via synaptic changes in the hippocampal system, a short-term memory (STM) which then supports reinstatement of recent memories into long-term memories (LTM) in the neocortex. The neocortical synapses change by a small amount on each reinstatement, which assures that learning, as a stochastic process, converges to the mean value of the statistical association of ensembles of experiences. The hippocampal system permits rapid learning of new items without disrupting the neocortex structure, and interleaves and integrates them into the neocortical system. In essence, the LTM is built-up incrementally from activation of STM. Furthermore, since extinction involves new learning, evidence suggests multiple memory systems may be applicable to the neural basis of extinction (Gabriele & Packard, 2006). We suggest the distal and proximal information streams which are contained in both PC and foraging models represent the STM and LTM system identified by neurological studies.

Forgetting is the other side of remembering and is important in PC models to explain spontaneous recovery. The idea being that the information stream acquired in the extinction phase is forgotten over time, which then removes the inhibition of the information streams acquired in the acquisition phase. This process is offered as an explanation for the stronger spontaneous recovery response that is observed with greater time between extinction and recovery tests and thus supports the view that learning in the extinction phase dissipates more rapidly than learning in the acquisition phase (Brooks & Bouton, 1993; Rescorla, 2004; Sissons & Miller, 2009).

Studies on forgetting provide valuable insight into its significance in associative learning. Recent memories are

vulnerable to interference from other mental activity and Wixted (2005) suggested that forgetting is largely a function of nonspecific *retroactive interference* acting on memory traces that have not yet consolidated in the neocortex. Wang & Morris (2010) hypothesized that extinction trials involve reactivation of the acquisition-trial memories in the absence of further reinforcement. However, such interactions can be complex and two memories may mutually exclude each other or coexist depending on the timing of the signal during extinction (Perez-Cuesta & Maldonado, 2009).

Decision making is treated differently in PC and foraging models. In foraging models, the decision to leave a patch is depends on which patch has the higher reward probability (maximizing) or is selected probabilistically (matching) (Kacelnik, Krebs, & Ens, 1987). PC models do not have choice-based decision rules and express the response rate as a monotonic function of the reward expectation. However, if PC and foraging have the same basis, then PC models contain a hidden decision rule in which the animal chooses between proximal and distal information. However, decision rules in both PC and foraging models are incomplete because psychology, ecology, neuroscience, and machine learning research show that uncertainty in the reward assessment is an important factor in decision-making (Daw et al., 2005; Platt & Huettel, 2008).

## The Model

We now develop a model for PC that has application to foraging models, draws on concepts from both modeling frameworks, and has some analogy to the neurology of decision-making. We model reward probability estimates for distal and proximal information streams, which correspond to the immediate patch and the surrounding habit in foraging models and to the short- and long-term estimates of rewards in PC models. We then combine the estimates with weightings based on their respective uncertainties. We also account separately for the process of learning that a signal can indicate a reward. Finally, we use the weighted expectation to model the animal's response rate in a trial.

### Distal and Proximal Reward Estimates

For each trial we define the distal and proximal expected reward estimate with a modified delta model,

$$\hat{x}_{j,i} = m_j y_i \delta_{j,i-1} + \hat{x}_{j,i-1} \quad (1)$$

where  $j = 1, 2$  indicates distal and proximal information streams,  $i$  designates a PC trial,  $m_j$  is the learning rate for stream  $j$ . For each stream the error between the expected reward probability and realized reward is

$$\delta_{j,i} = x_i - \hat{x}_{j,i} \quad (2)$$

where  $x_i$  is a reward/no-reward outcome (0,1) for trial  $i$ . The term,  $y_i$ , is a measure of the strength of the association of the signal-reward and is independent of reward probabilities. For convenience, we consider the distal and proximal information streams *unconscious* reward estimators because individually they are sub-process that must be combined to

affect the animal's response. We designate the combined estimator the *conscious* reward estimate.

### Combined Estimate

The distal and proximal estimates of reward probability are combined into a single conscious reward estimate that the animal uses in making decisions:

$$\tilde{x}_i = w_{1,i}\hat{x}_{1,i} + w_{2,i}\hat{x}_{2,i} \quad (3)$$

where the estimates are combined according to their respective weighting factors that depend on their associated uncertainties  $\tilde{\delta}_{j,i}^2$ . As we develop next, the uncertainties are in fact EWMA's of the variance in the distal and proximal estimators and so the estimates can be combined using a standard statistical weighting formula in which the weight for estimate  $j$  on trial  $i$  is

$$w_{j,i} = \left(1/\tilde{\delta}_{j,i}^2\right) / \left(1/\tilde{\delta}_{1,i}^2 + 1/\tilde{\delta}_{2,i}^2\right). \quad (4)$$

It is noteworthy that this weighting scheme is not found in either PC or foraging models.

### Temporal Discounting Uncertainty

The uncertainties used in weighting,  $\tilde{\delta}_{j,i}^2$ , are developed from the mean-squared errors of the distal and proximal reward estimates. Of relevance, the uncertainties depend on the time between trials as follows. First, compute unadjusted uncertainty estimates as EWMA's from errors defined by eq. (2):

$$\hat{\delta}_{j,i}^2 = n(\delta_{j,i-1}^2 - \tilde{\delta}_{j,i-1}^2) + \tilde{\delta}_{j,i-1}^2, \quad (5)$$

where  $n$  is the uncertainty learning rate. Next, adjust the uncertainties for the time interval  $\Delta t = t_i - t_{i-1}$  between trials:

$$\tilde{\delta}_{j,i}^2 = \hat{\delta}_{j,i}^2 h_j^{\Delta t} \quad (6)$$

where  $h_j$  is a decay parameter that controls the rate at which the uncertainty in information stream  $j$  decays as time between trials increases. In this model, as the inter-trial time increases, we want to put more confidence on the distal (long-term) estimate and less on the proximal (short-term) estimate. The idea being that in a sequence of trials with uncertain outcomes, as time passes since the last trial we should trust the long-term estimate of reward probability more than the short-term estimate based only on the last few rewards. To insure this shift in confidence to the distal estimate, we decay the distal uncertainty but not the proximal uncertainty as time passes between trials: Mathematically this is achieved with  $0 < h_1 < 1$  and  $h_2 = 1$ .

### Signal-Reward Association

The term  $y_i$  in eq. (1) tracks the strength of the signal-reward association, which we assume is distinct from probability learning but also depends on the error of predictions. Learning requires repetition and reduction of errors in prediction, and we model these properties with a three step process. First, we track conscious error based on the difference between the trial outcome and the conscious expectation from eq. (3) giving

$$\delta'_i = x_i - \tilde{x}_i. \quad (7)$$

Second, because errors are by nature random and one correct prediction,  $\delta'_i = 0$ , is insufficient to develop an association, we compute an average error with a EWMA:

$$\tilde{\delta}_i^2 = n(\delta_{i-1}^2 - \tilde{\delta}_{i-1}^2) + \tilde{\delta}_{i-1}^2. \quad (8)$$

where  $n$  is again the uncertainty learning rate. Third, to capture the repetitive and asymptotic nature of appetitive learning, we incrementally accumulate the uncertainties with a standard saturation function

$$y_i = \sum_{k=1}^{i-1} 1/\tilde{\delta}_k^2 / \left( g + \sum_{k=1}^{i-1} 1/\tilde{\delta}_k^2 \right) \quad (9)$$

where  $g$  is the halfway point in the learning process.

### Response Rate

We relate the conscious reward expectation to the response rate with a matching function that asymptotically increases a response from a background level to a maximum and is defined with scale and shape parameters  $r_{max}$  and  $r$  as

$$R = r_{max} \tilde{x}_i / (\tilde{x}_i + r(1 - \tilde{x}_i)). \quad (10)$$

### Parameter Summary

The complete model combines elements of classical associative learning and patch foraging. While several models contain multiple memory streams that track information over different time scales, the model presented here tracks the uncertainties in the estimates as information streams as well. The model contains 7 parameters (Table 1).

Table 1: Model parameters and values fitted to data.

Parameter	Fitted value	Meaning
$m_1$	0.055	Distal learning rate
$m_2$	0.248	Proximal learning rate
$n$	0.075	Uncertainty learning rate
$h_1$	0.126	Distal uncertainty decay rate
$g$	971	Association half-way constant
$r_{max}$	6.88	Response function scale parameter
$r$	0.13	Response function shape parameter

### Comparison to Experiment

To demonstrate the flexibility and perspective the model provides, we fit it to a study of partial reinforcement extinction conducted by Haselgrove, et al. (2004). We selected this experiment because PREE is difficult for PC models to explain. In addition, the study covers an acquisition phase and two extinction phases, which demonstrate spontaneous recovery. Several models produce these basic patterns but not when one of the groups is trained with partial rewards.

In the experiment, rats divided into partial and continuous reinforcement groups received the same signal and number of rewards during an acquisition phase in which the reinforcement schedules differed. In the partial group, half of the trials were reinforced with two rewards, while in the continuous group one reward was given on every trial. Following the acquisition sessions, the rats received two sessions with unreinforced signals. In Figures 1-3, each point designates an entire session in the acquisition phase, while each point represents a block of two trials in the two extinction sessions following.

We fit the model to the data from both groups with a single set of parameters (Table 1) using the “mco” package in the R statistical programming language. This is a multi-criteria optimization algorithm based on a genetic algorithm ([cran.r-project.org/web/packages/mco/mco.pdf](http://cran.r-project.org/web/packages/mco/mco.pdf)).

The model fit the response patterns for the continuous and partial groups reasonably well. The mean responses in the acquisition phase developed in a similar manner for both groups, while in the extinction phase the continuous group response decayed more rapidly than the response in the partial group. Both groups exhibited spontaneous recovery in the final extinction session with the continuous group response again decaying faster than the partial group response (Figure 1).

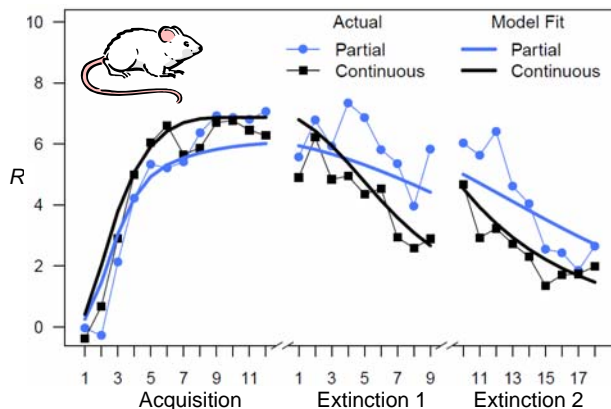


Figure 1: Haselgrove et al. (2004) data and model fit for partial and continuous reinforcement groups using parameter values in Table 1.

## Discussion

The patterns of the underlying streams producing the fit to the Haselgrove et al. (2004) data for the continuous reinforcement group (Figure 2) and the partial reinforcement group (Figure 3) illustrate how a framework of multiple-scale estimators and uncertainties can account for seemingly complex patterns in PC studies. As in Figure 1, the first section consists of session averages for the acquisition sessions, and the next two sections each represent an extinction session in blocks of two trials.

**Continuous Reinforcement Group** In Fig. 2a the signal-reward association strength,  $y$ , rises over the acquisition phase to its full value and remains constant thereafter, implying that the animal has fully learned the association. The conscious reward probability also reaches its full value in the acquisition phase and then exponentially declines in the extinction phases. At the beginning of the second extinction phase, the expectation is higher than at the end of the first extinction phase, then the expectation again decays since the animal receives no rewards. This somewhat complex pattern of responses is generated by a unique weighting of relatively simple patterns in the distal and proximal estimators. The proximal estimator (Figure 2b), which is generated by a faster learning coefficient, rises quickly in the acquisition phase and then decays quickly in the first extinction phase and remains at zero throughout the second extinction phase. The distal estimator, being the slow learner, rises slowly in the acquisition phase and then decays slowly over the next two phases. The pattern in the weights (Figure 2c) that mix the two estimators produces the spontaneous recovery. Beginning in the acquisition phase, the weightings are equal. Because rewards are consistently received, the proximal estimator quickly adjusts and has less uncertainty than the distal estimator, giving the distal estimator the greatest weight in forming the conscious estimator in eq. (4). In the period between the acquisition and extinction phases, eq. (6) decays the distal uncertainty (trust the long-term estimate when information is old), so the two weights are nearly equal beginning the extinction phase. However, as signals are consistently unrewarded, the proximal estimator better represents the environment and its weight rises over the trials. The distal uncertainty decays again after the first extinction phase, and the pattern is repeated in the second extinction phase. At the beginning of the second extinction the proximal estimator, which predicts a reward, has a higher weight than the distal estimator, which predicts no reward, so the animal exhibits spontaneous recovery.

**Partial Reinforcement Group** In the acquisition phase, the patterns of conscious expectation and the signal-reward association (Figure 3a) are similar to the patterns in the continuous reinforcement group (Figure 2a), although the strengths are half the continuous reinforcement values. The patterns in the distal and proximal estimators are similar also (Figure 3b), and again the strengths are about half showing the accurate estimation of the 50% reward probability during acquisition. However, the experiments differ significantly in the weighing function patterns. These are reversed in the partial reinforcement group (Figure 3c) compared to that in the continuous reinforcement group (Figure 2c). This difference drives the differences in the response patterns (Figure 1). Again, at the beginning of the experiment, the distal and proximal uncertainties are equal, making for equal weights. However, both estimators

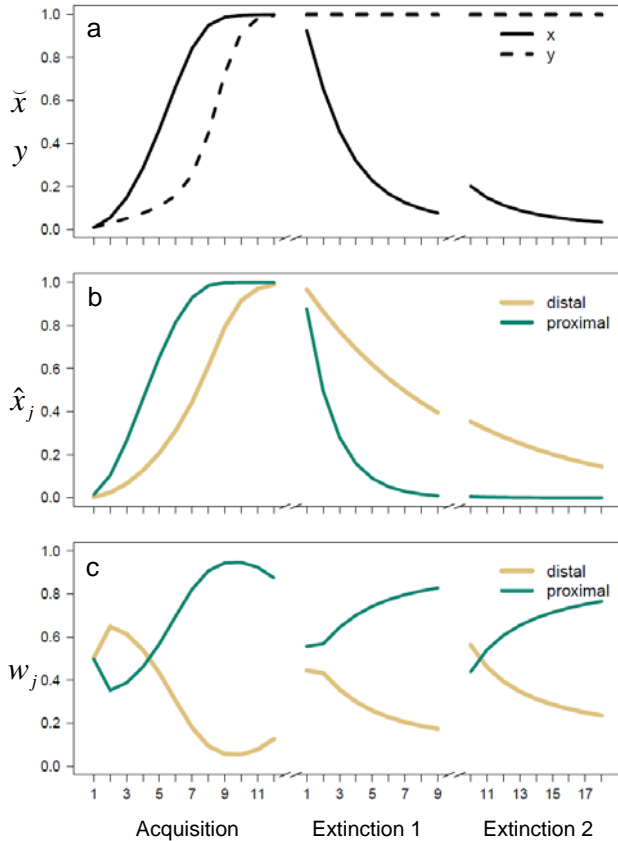


Figure 2: Changes in model variables for the continuous reinforcement group.

have higher uncertainty with partial reinforcement, but the proximal estimator, which is strongly influenced by the previous trial, has higher uncertainty than the distal estimator, which integrates the reward expectation over multiple trials. The result is lower uncertainty for the distal estimator and thus greater weight in forming the conscious estimator. Between the acquisition and extinction phases, the distal uncertainty declines while the proximal uncertainty is fixed, so the distal estimator is dominant at the beginning of the first extinction phase. Over the phase the distal uncertainty increases while the proximal uncertainty decreases until they are equal at the end of the extinction. Therefore, at the end of the extinction phase, the animal has a higher response rate than in the continuous case, which is dominated by the proximal estimator. Between the first and second extinction phases, the distal estimator uncertainty again decays giving it more weight in the second extinction phase, resulting in a higher response and slower decline in response for the partial acquisition group.

### Neurological Analogies

As our ultimate goal is to model the brain, not just observed behavior, we seek to identify possible equivalences between the model's elements and neural structures as has been encouraged by Rangel et al. (2008) and others. In a broad

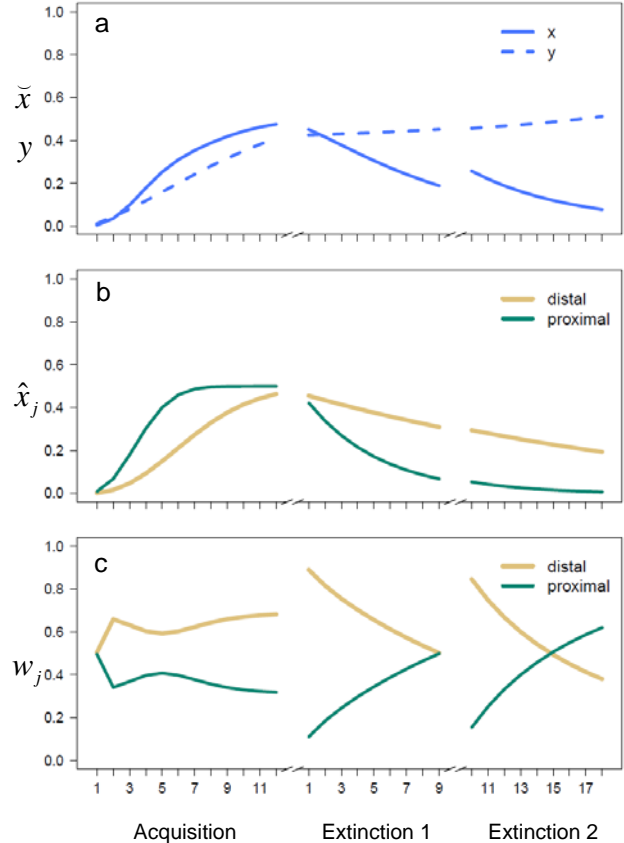


Figure 3: Changes in model variables for the partial reinforcement group.

sense, we suggest that the distal and proximal information streams  $\hat{x}_{1,i}, \hat{x}_{2,i}$  represent parallel memory systems that characterize reward probabilities estimated on different temporal scales. These terms might be candidates for STM-LTM systems involving the hippocampus and neocortex. However, the two streams are competitive and so they might be representative of competitive memory systems such as the hippocampus and basal ganglia (White & McDonald, 2002; Poldrack & Packard, 2003). In our model the signal-reward association  $y_i$  represents a separate memory stream that builds in a cumulative manner by summing the inverse of trial-by-trial uncertainties. This incremental building of memories is also a feature of the STM-LTM interaction of the hippocampus and neocortex (McClelland, McNaughton, & O'Reilly, 1995).

Uncertainty is specifically formulated in our model, and neural structures are clearly involved with uncertainty in decision-making. For example, Doya (2008) noted uncertainty has two flavors: one resulting from the environmental stochasticity (risk) and one from the limited knowledge of the decision-maker (ambiguity). Studies suggest that risk is represented in the striatum and precuneus while ambiguity is represented in the lateral orbitofrontal cortex and amygdala (Platt & Huettel, 2008). Our model also has two flavors of uncertainty. The

uncertainty in the distal and proximal reward estimators  $\hat{\delta}_{j,i}^2$  tracks variability in the environment that we suggest is akin to risk uncertainty. The uncertainty in signal-reward association  $\bar{\delta}_i^2$  is a candidate for the decision-maker's ambiguity.

## Final Thoughts

Under the assumption that animals in laboratory studies use behavioral strategies and neurological processes that evolved through natural selection, we reconsider Pavlovian conditioning in the context of animal foraging. From this perspective, animal behavior in a constrained environment has a hidden spatial component that leads us to consider the behavior in terms of distal (habitat) and proximal (local patch) information streams. In this framework the animal does not track distinct memory streams for acquisition and extinction phases, which we suggest is the experimenter's perspective. Instead of having to know when the experimenter ends one phase and starts another, the animal can view the environment as continuous yet random and simply track information measuring over two different time scales and weighting the estimates according to the trial-by-trial changes in their uncertainties.

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