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Tracking a changing environment: optimal sampling, adaptive memory and overnight effects

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Abstract

Foraging in a variable environment presents a classic problem of decision making with incomplete information. Animals must track the changing environment, remember the best options and make choices accordingly. While several experimental studies have explored the idea that sampling behavior reflects the amount of environmental change, we take the next logical step in asking how change influences memory. We explore the hypothesis that memory length should be tied to the ecological relevance and the value of the information learned, and that environmental change is a key determinant of the value of memory. We use a dynamic programming model to confirm our predictions and then test memory length in a factorial experiment. In our experimental situation we manipulate rates of change in a simple foraging task for blue jays over a 36 hour period. After jays experienced an experimentally determined change regime, we tested them at a range of retention intervals, from 1 to 72 hours. Manipulated rates of change influenced learning and sampling rates: subjects sampled more and learned more quickly in the high change condition. Tests of retention revealed significant interactions between retention interval and the experienced rate of change. We observed a striking and surprising difference between the high and low change treatments at the 24 hour retention interval. In agreement with earlier work we find that a circadian retention interval is special, but we find that the extent of this ‘specialness’ depends on the subject’s prior experience of environmental change. Specifically, experienced rates of change seem to influence how subjects balance recent information against past experience in a way that interacts with the passage of time.

Keywords

tracking; sampling; memory; environmental change; foraging; blue jays

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Introduction

Animals live in a changing world. Some change occurs predictably (e.g. daily and seasonal patterns) but much of this change occurs unpredictably. Animals often need to respond to this change. For example, they must adjust their behavior to a change in prey quality or the presence of a predator. Adjusting to a changing world is a two part problem. The animal must somehow use experience to obtain information about the current state of the world (which we call ‘tracking’), and the animal must somehow retain this information and translate it into appropriate action. Taken together these two aspects of the ‘adjusting to change’ problem call upon nearly every aspect of an animal’s cognitive machinery from perception to decision-making. As a crude caricature however, these two functional processes crudely coincide with learning and memory. When the animal tracks the environment, it learns about the states of the environment as it experiences changed conditions. Similarly, when animal later acts on this in response to this experience, it must call upon some ‘stored’ or remembered representation of this experience. In practice, we cannot separate these two aspects of the problem. We cannot investigate the retention of information unless the animal has acquired it previously; and we cannot investigate the acquisition of information unless the animal retains it in some way. The intimate relationship between learning and memory will be familiar to many students of animal psychology. Yet, as a matter of research strategy, it is often convenient to focus on either the acquisition or retention side of the problem in any given study.

For example, several models have been used to apply ideas from behavioral ecology and foraging theory to the acquisition side of this problem under the general heading of environmental tracking (reviewed in Stephens 2007; Stephens and Dunlap 2008). These models are typically used to ask how frequently an animal should ‘sample’ the resources in its environment to optimally adjust its behavior to changing conditions. Obviously enough, the degree and nature of environmental change is a fundamental part of these models. Qualitatively, both low and high rate of change can reduce the value of environmental tracking. If the environment never changes, the animal can adapt to it genetically and so it doesn’t need a learning-like mechanism. On the other hand, if the environment changes unpredictably there is literally nothing to track, and again the animal doesn’t need a tracking mechanism. Between these two extremes, we expect that higher rates of change will necessitate higher sampling effort. Theoretically, the relative costs of errors of sampling too much (checking resources too frequently in a stable environment) and sampling too little (checking too infrequently and missing the opportunity to exploit a profitable environmental change) interact with the rate of change in the environment to determine the optimal degree of sampling effort. This body of theory is relatively mature, and we now have several experimental studies of these models (see Stephens 2007 for a review). Curiously, most of these experiments have manipulated the theoretically important ‘cost of error’ variables, and not the more fundamental environmental rate of change.

In contrast to the acquisition side of the problem, behavioral ecologists have paid relatively little attention to the output or recall side of the tracking problem. A few models have addressed this problem by modeling the fitness value of memory, typically linking this to environmental variability in a relatively obvious way: long-lasting memory does not pay

when environments change quickly because information go ‘out of date’ when things change quickly (e.g. Anderson and Schooler 1991; Dunlap et al. 2009). These models commonly consider how a memory system should integrate old and new experience. In doing this, they use a range of mathematical weighting schemes (e.g., exponential weighting, linear operators or Bayesian analysis) to explore past vs. recent balance (e.g. Devenport et al. 1997; Harley 1981; Houston et al. 1982; Killeen 1981; Valone 2006). These ‘weighted memory’ models commonly predict that animals should give more weight to recent experience in changing environments. The rationale for this result clearly follows the same logic as in memory length models: in changing environments old information becomes ‘out-dated’ quickly (Mangel 1990; McNamara and Houston 1985; McNamara and Houston 1987). Empirical work that addresses the fitness value of memory is relatively rare, although there are many snippets within the larger literature of learning and memory that bear on it in one way or another. A simple and elegant series of studies by Devenport and Devenport shows how empirical studies might proceed by testing how animals weight new versus old information, and qualitatively supports the ideas developed within this paper (1994; 1997).

Within these models, change is an abstraction. They can accommodate change occurring at arbitrary time scales. In nature, however, some time scales are more important than others. Daily and annual cycles, for example, surely impose some structure on the types of changes that matter to animals in nature. Many readers will know that periods of 24 h are special in several ways, both physiologically and behaviorally. Animals seem to recall events that happen at 24 h intervals more accurately in some experimental situations (e.g. Daan 2000; Pahl et al. 2007; Prabhu and Cheng 2008a; Zhang et al. 2006). Yet, models of tracking and adaptive memory do not incorporate these special intervals. In practice this may be because experimental studies of tracking focus on relatively short time intervals (i.e. less than a day), but surely animals face the problem of tracking at many different time scales so a general exploration of this problem must consider both long and short-term environmental changes. Consider the difference between an animal adapted to high rates of change and another adapted to low rates of change. Even without a formal model, we expect that animals in environments with high rates of change should track their environments relatively closely, and they should respond to changes relatively quickly. Animals in high-change conditions should also devalue old information, because high rates of change mean the information becomes outdated quickly. In contrast, animals adapted to lower change rates should adjust to changed condition more slowly and rely more heavily on old information. This paper tests these intuitive claims about the acquisition and retention of information via dynamic programming model and a straightforward factorial experiment. We first modeled our specific experimental scenario to confirm the general predictions from the literature, and then tested captive blue jays in two change regimes (high and low change rates). To assess how these rates of change influenced the jay’s sensitivity to aging information, we tested five different retention intervals, creating a 2 by 5 factorial experiment with two levels of change rate, and five levels of retention interval.

Model

We first model a simple scenario considering an animal choosing between two stimuli, with this choice being repeated across a series of trials (time steps). At any given trial, the subject

can select stimulus A or stimulus B. Only two situations are possible: A correct and B wrong, or A wrong, B correct. We call these the A correct and B correct states. We assume that a symmetric persistence process governs the transition between these two states, with q giving the probability of remaining in the same state (and $1-q$ the probability of switching correct states). In the absence of complete unpredictability, it would seem that there is nothing to track in this situation because an animal can immediately recognize which state is true. For instance, if the subject samples stimulus A and fails to obtain a reward, then it should immediately switch to choosing stimulus B (because only one stimulus can be correct at a time). It is a simple, but likely unrealistic, result that assumes animals can perfectly recognize the current state (A or B correct), and this is a difference from previous models. Instead, we distinguish between the true state and the recognized state. We do this using an error rate, ε , which we define as the probability that the recognized state differs from the true state.

We solved this problem using dynamic optimization, first determining the optimal behavior in the final time step, and then using this value to determine the optimal behavior for each prior time step. Let p be the subjective probability of the A correct state. In the final time step, then, the optimal behavior is to choose A if $p \geq 1/2$, with a payoff of p , and to choose B if $p < 1/2$, with a payoff of $1-p$. The optimal payoff for the last time step is a function of p , which we'll call $V_0(p)$. This takes the form of a simple V shape.

Solving the second to last step is a bit more complicated. The payoffs are the same (choose A, get p ; choose B, get $1-p$). Regarding the state variable, p , four things can happen: either A or B could be true, and each could either be correctly or incorrectly recognized (Table 1):

The animal, however can only subjectively observe two events: recognizing A or recognizing B, and these occur regardless of the actual choice the subject makes (Table 2).

If A is recognized, we can find the probability that A is true by Bayes Theorem:

$$P(A_{correct}|A_{recognized}) = \frac{P(A_{rec}|A_{cor})P(A_{cor})}{P(A_{rec}|A_{cor})P(A_{cor}) + P(A_{rec}|B_{cor})P(B_{cor})} \quad [1]$$

$$p' = \frac{(1 - \varepsilon)p}{(1 - \varepsilon)p + \varepsilon(1 - p)} \quad [2]$$

Similarly

$$P(A_{correct}|B_{recognized}) = \frac{\varepsilon p}{\varepsilon p + (1 - \varepsilon)(1 - p)} \quad [3]$$

We now add change to this basic framework. Given p , the probability that A is correct in the next time step is:

$$Q(p) = p'' = q \cdot p' + (1 - q)(1 - p') \quad [4]$$

Let $V_A(p)$ be the value of choosing A and let $V_B(p)$ be the value of choosing B. This is the value of the memory of this information. So:

$$V_A(p) = p + [(1-\varepsilon)p + \varepsilon(1-p)] \cdot V_0 \left[Q \left(\frac{(1-\varepsilon)p}{(1-\varepsilon)p + \varepsilon(1-p)} \right) \right] + [p\varepsilon + (1-p)(1-\varepsilon)] \cdot V_0 \left[Q \left(\frac{\varepsilon p}{\varepsilon p + (1-\varepsilon)(1-p)} \right) \right] \quad [5]$$

$$V_B(p) = (1-p) + [(1-\varepsilon)p + \varepsilon(1-p)] \cdot V_0 \left[Q \left(\frac{(1-\varepsilon)p}{(1-\varepsilon)p + \varepsilon(1-p)} \right) \right] + [p\varepsilon + (1-p)(1-\varepsilon)] \cdot V_0 \left[Q \left(\frac{\varepsilon p}{\varepsilon p + (1-\varepsilon)(1-p)} \right) \right] \quad [6]$$

We give $V_1(p)$ as the optimal behavior when two steps remain, and

$$V_1(p) = \max[V_A(p), V_B(p)] \quad [7]$$

We use V_0 to calculate V_1 , and since the logic for the second to last time step applies generally, we can calculate $V_n(p)$ from $V_{n-1}(p)$ in the same way. We solved the problem numerically by finding $V_i(p)$ for a list of p values, and then found $V_{i+1}(p)$ using the previously calculated values of $V_i(p)$.

Figure 1 represents a typical result from the model. In general, V declines: memory loses value more quickly when persistence, q , is low (and the value starts out at a lower point). In investigating the effects of changing parameters on the results, we find that changes in error rate have little effect, except when error rates are extremely high (e.g. $\varepsilon=0.5$) and the world is completely persistent ($q=1.0$). In this case, the surface becomes a much more pronounced V-shape across all of the time steps. To demonstrate the effects of varying the rate of change, we divide the value of memory (V) by time step. We find that as time steps increase, the rate converges upon the persistence value, q (Figure 2). From these results in general, we expect better memory at shorter intervals because animals should be more closely following their most recent experience. This simple two-choice model, where the value of one item implies the value of the second item, qualitatively agrees with the differently structured memory models of the past: increasing change decreases the value of memory across time.

Materials & Methods

In this experiment, our experimental subjects acquired information under an experimentally determined regime of environmental change for a day and a half. We then tested their choice following a single interval of time. By repeating this procedure many times, under both high and low levels of change, we generated mean choice data for each bird for each of 5 different time intervals in both high and low change treatments.

Subjects & Experimental Apparatus

Eight adult blue jays (*Cyanocitta cristata*) of unknown sexes and mixed experimental histories served as subjects. These birds were captured from the wild as nestlings and were hand reared in the laboratory. All birds were between three and ten years old. We tested the birds in operant boxes (Fig 3). Each box was equipped with two stimulus projectors in the front of the box and one stimulus projector in the rear. We placed a hinged perch attached to

a micro switch under each stimulus projector so that we could determine when the subject hopped to each perch. Choice of a stimulus was registered as a hop to the perch beneath the projector. We attached a pellet feeder to each box, and food was delivered to a cup in the front of each box, located between the two stimulus projectors. A small light in the food cup (a magazine light) flashed with each food delivery. A computer controlled all the equipment, ran the programmed experimental contingencies and collected the resulting data. Prior to the experiment, we trained the birds to perform in the operant boxes using shaping techniques whereby we trained each bird in successive approximations to acquiring food by hopping towards flashing lights.

We used a modified closed economy system, in which birds received all of their daily food within the experimental trials. This allows each bird to experience the consequences of their choices: good choices resulted in more food, poor choices in less. Birds performed in the experiment for 8 hours each day, and remained in their boxes for 23 hours each day. We removed the birds for one hour each afternoon to clean the boxes, save the data, and weigh the bird and check its health. To ensure that each bird stayed in good health, we set a minimum amount of food a bird would receive each day (determined by the weight maintenance of each bird). In the very rare case that a bird did not achieve the minimum on any day, we fed the bird the difference between the amount gained in the box during trials and the minimum allowance.

Basic Experimental Design

To create an environment in which we could easily manipulate 'environmental change' our experiment used a two-choice reversal learning task. In this situation, the animal learns a relatively simple discrimination task in which choosing one stimulus (say stimulus A) leads to food and choosing another (say stimulus B) does not. Reversals occur because at experimentally determined times we reversed the effects of the two choices so that after a reversal stimulus B leads to food and stimulus A does not. We changed the frequency of reversals to create different regimes of environmental change. Using this basic framework, we tested hypotheses about the acquisition and retention of information in changing environments. To do this, birds experienced three phases of trials (Fig. 4). In the first phase, the birds performed in the reversal learning task, in some cases experiencing a high change treatment (frequent reversals) and in others experiencing a low change treatment (infrequent reversals). In the second phase all birds in all treatments experienced a final stimulus reversal, and these conditions persisted until the bird chose correctly five times in a row. After reaching the five-in-a-row criterion, the third phase of trials began, during which we tested retention of previous acquired information.

We randomized the order of the high and low change treatments, such that the order was balanced across the eight birds. Within each change treatment for each bird, we randomized the retention intervals tested in four blocks of five intervals each (one of each interval in each block). We did this to ensure that any order effects within the probes tested would be balanced across the retention intervals.

Testing a Single Retention Interval

Each stimulus was a combination of a color (red, blue, green, or yellow), and a shape. We always presented the stimuli as pairs, with the computer randomly determining the side each stimulus appeared on in each trial. Each learning trial began with the rear light flashing, upon which, the bird hopped to the rear perch. Once the bird was on the rear perch, the computer presented the stimuli flashing on the front projectors. A choice was registered by a hop to the perch below the stimulus, at which point both stimulus lights extinguished and the bird would either be fed one pellet, or fed no pellets. A correct choice was followed by an intertrial interval (ITI) of 40 seconds, while an incorrect choice was followed by a longer ITI of 120 seconds. At the end of the ITI, the rear light flashed, beginning a new trial. A trial would abort and begin anew following any 20 minute period of inactivity.

The computer determined which stimulus would be rewarded, and the reward stimulus remained the same until an experimentally determined reversal occurred. In the low change treatment, the rewarded stimulus changed only once, five hours after the start of a new treatment. In the high change treatment, the computer drew the time between reversals from a normal distribution with a mean of 60 min, with a new time chosen after each change interval. The birds performed learning trials for eight hours during the first day of testing a new retention interval and then during the morning of the next day. We extended the trials across two days to allow adequate experience with the treatments and to allow the testing of 1 and 4 hour retention intervals (which would otherwise run into the dark period for the birds).

Following 2 hours of learning trials on the second day, the rewarded stimulus would switch for a final time for both treatments. We then tested the birds for learning the new stimulus values to a criterion of five correct rewarded trials in a row. We chose this criterion based on pilot data. Once the bird met this criterion, the computer would switch the bird to a simple light following task. In this task, a trial would begin with the rear white light flashing. The bird would hop to the rear perch and then only one of the front white lights would flash. Birds hopping to the perch in front of the flashing light would be rewarded. This task would continue for eight hours each day until the retention interval was reached. Upon reaching the end of the retention interval, the apparatus again presented the A and B stimuli the bird experienced in the final learning set (with rewarding and non-rewarding stimuli set as in the final learning set). The bird's choice in this situation provides our basic information about the effects of change on the retention of information (i.e. memory). After making this final choice, the bird continued in the simple light following task until the end of the experimental day.

On the following day the bird would begin the learning trials for the next retention interval. To reduce the effects of interference between tests of retention intervals, we selected a new stimulus pair for the each new retention interval test. We randomly selected a sequence of 14 stimulus pairs before the experiment.

Dependent Measures

We used two measures to look at how birds track changes, and one to assess retention of their most recent experience. We tested our predictions about the effects of change on tracking behavior in two ways. First, we used the relative frequency of ‘incorrect stimulus’ as a broad measure of sampling behavior. We calculated this relative frequency over the first 8 hours of each treatment; when the bird was gaining experience about the rate of change. The rationale for this is that when a reversal occurs, a subject must use its experience of both rewarded and non-rewarded options, so we interpret at least some of these incorrect choices as sampling or checking the state of the environment. Second, we assessed the ability of subjects to track changes by asking how quickly they reached our criterion for ‘correct’ behavior in the final reversal of each treatment (recall that this reversal was identical for all birds in all treatments). To assess our subject’s retention of information (i.e. memory), we measured the relative frequency with which choice matched the subject’s most recent experience (i.e. which stimulus was correct at the end of the final learning set).

Results

Sampling the Environment

Our first analyses ask how the birds sampled the experimental environments. To begin, we performed a crude analysis of differences in tracking by examining choice behavior during the first day of learning trials for each new stimulus pair. We predicted that birds in the high change treatment sample the non-rewarding stimulus more frequently than birds in the low change treatment. At the largest scale of analysis, we can look across each entire first learning day at how often birds sampled the unrewarded stimulus. Birds chose this unrewarding option more frequently in the high change treatment (unrewarded choices/day $\bar{X} \pm SD$, high change= 103.60 ± 32.60 , low change = 46.36 ± 20.68 ; Paired t-test: $t_7 = -8.987$, $P < 0.0001$).

Birds could be sampling, in the traditional sense of acquiring new information, but they could also be making overrun errors, which occur when stimulus values change and an individual continues to choose the now unrewarding stimulus. Our next analysis, therefore, takes a more restrictive view by comparing the choices of the unrewarding stimulus (what we are calling sampling) during periods in which no stimulus changes occurred. To control for time of day effects, we chose the closest 20-trial interval with no stimulus value change occurring before 1400 on the first day of learning each new stimulus pairing. We chose this time to correspond roughly to the stimulus value change occurring in the low change treatment. Even with the more stringent criteria, we still found a statistically significant difference between the environmental variability treatments, with birds sampling more frequently in the high change treatment than in the low change treatment (errors in 20 trial sample, $\bar{X} \pm SD$, high change= 2.833 ± 1.08 , low change= 0.532 ± 0.383 ; Paired t-test: $t_7 = -7.30$, $P < 0.0002$).

Tracking Change in the Environment With Learning

To assess how well the birds tracked the environment, we compared how many trials birds required to reach the learning criterion (5 correct trials in a row) during the final learning set

for each stimulus pairing. A quick adjustment to this final change indicated “good tracking,” while a slower adjustment indicated less effective tracking. As predicted, birds reached the learning criterion more quickly during the high change treatment (mean trials to criterion $\bar{X} \pm SD$, high change = 17.218 ± 7.620 , low change = 31.696 ± 16.534 ; Paired t-test: $t_7 = 3.16$, $P < 0.016$).

In the high change treatment, birds tracked the environment more efficiently, requiring a smaller number of trials, but across the 10 previous hours of experience they also had many more changes to track. In a highly variable environment, like our high change treatment, foragers must track to maintain an adequate intake rate. Did our birds track the environment well enough to keep up with their rate of food intake under the low change environment? We measured the average rate of food gain for each bird during the first day of learning trials under each of the environmental change treatments. Birds obtained a higher rate of food gain under the low change treatment (g/min $\bar{X} \pm SD$, high change = 0.0126 ± 0.0026 , low change = 0.0179 ± 0.0013 ; Paired t-test: $t_7 = 5.899$, $P = 0.0006$). A higher level of tracking did not completely offset the losses incurred due to the changes in the variable environment (theoretical max is 0.0279 g/min, both low and high significantly differ from this maximum, $P < 0.05$).

Memory and Choice of the Last Experienced Stimulus

In all treatments, birds completed the final learning set with levels of discrimination that satisfied our criterion. The next stage of our experiment asks whether their earlier experience with different levels of environmental experience affected their retention of information. As described in the methods, we assessed this with probe trials at the five different retention intervals. We first asked whether birds chose according to their most recent experience. A correct choice according to their most recent experience would be to choose the stimulus that was rewarded during their final learning set. Figure 5 shows the mean choices for each treatment and retention interval. The figure shows a striking interaction between retention interval and environmental change. While the behavior is similar in the high and low change treatments at short retention intervals, we see a striking difference at the 24 h retention interval. In high change treatments the jays followed recent experience much more frequently than in low change treatments. In support of this interpretation, a repeated measures ANOVA found a significant interaction between the main effects of treatment and interval ($F_{(4,28)} = 2.77$, $P < 0.048$, our ANOVA found no other significant effects).

We analyzed this further using contrasts. Within the high change treatment the dramatic change from 4 hrs to 24 hrs is statistically significant ($F_{(1,7)} = 14.00$, $P = 0.0072$). The next change, from 24 hrs to 48 hrs, was also statistically significant ($F_{(1,7)} = 7.06$, $P = 0.032$). The most striking difference was between the performance of birds in the low and in the high change treatments after 24 hrs. This difference was significant, with birds choosing correctly in the high change treatment, but incorrectly in the low change treatment ($F_{(1,7)} = 11.67$, $P = 0.011$).

Thus, birds in the low change treatment chose no differently after 1 hour than they did after 4 hours; however birds chose much less accurately (according to their most recent

experience) at 24 hrs. In the high change treatment, birds made more accurate choices after 1 hr, less accurate choices after 4 hrs, and their best choices of all following 24 hrs. In both treatments, we saw similar choices after 48 and 72 hrs, an increase in performance from 24 hrs for birds in the low change treatment, but a decrease in performance from 24 hrs for birds in the high change treatment.

Following a full day and presumably overnight consolidation of the previous day's memories, birds in the high change treatment chose the most recent stimulus most frequently. But, birds in the low change treatment tended to choose more towards the opposite: the stimulus, which had not been rewarded most recently (but which had been rewarded for the longer period of time that previous day, see figure 5).

Balancing Recent with Past Information

The results in Figure 5 suggest a classic problem in the 'tracking' literature: how do animals weigh recent versus past experience. Our design seems to preclude a direct analysis of this question, because we have no reason to think that past experience should bias choice in one direction or the other (this is because we took pains to ensure that subjects had equal amounts of experience with both environmental states in the 'change' treatments). However, while we equated experience in terms of trials (subjects experienced the same number of trials for each stimulus condition), there is one situation in which a condition remained true for a longer than normal period of time. This situation occurs when the stimulus that was 'correct' at the end of day 1 remained 'correct' at the beginning of day 2, and this might produce a bias in favor of this 'correct overnight' situation. This seems especially likely given the results of figure 5 which suggest that overnight processes (e.g. memory consolidation) may be quite important. With this idea in mind, we performed an analysis that pitted sensitivity to this 'overnight correct' state (which is our proxy of 'past experience') against sensitivity to the correct state at the end of the final learning trials (our proxy for 'recent experience').

To perform this analysis, we examined all instances where the past information (the overnight correct stimulus) and recent information (most recently correct stimulus) conflicted. Using this subset of our data, we calculated a past-recent index which gives normalized measure of our subject's sensitivity to past vs. recent experience. To calculate this index, we first counted the number instances for each bird, where recent and past information conflicted. This was always the same number for low change, but varied due to chance with high change. We then divided those numbers of instances by what we would expect by chance for the number of conflicted trials available in each case. Figure 6 shows our analysis graphically. The figure shows an impressive difference between the high and low change treatments, which seems to be nearly mirror images of each other. In support of our impressions, a repeated measures ANOVA shows a significant interaction between change treatment and retention interval ($F_{(4,28)} = 3.68$, $P = 0.0157$, the ANOVA shows no other significant effects).

We performed a series of post hoc tests to explore the nature of the interaction between change treatment and retention interval. Although the figure draws one's attention to the difference at the 24 h retention interval, our post hoc analysis suggests that the difference at

short retention intervals (specifically 1 h) may be more important. Specifically, at a 1 h retention interval the difference between high and low change treatments is significant ($F_{(1,7)} = 7.716$, $P = 0.0273$). Our subjects favored ‘past experience’ at short retention intervals in the high change treatment, yet they chose at chance levels in the low change treatment. In contrast, in the high change treatment, birds after 24 hrs chose the stimulus that was rewarded most recently, and they did so even when this conflicted with what was the best stimulus from the past (the overnight correct stimulus before the second day of learning). But, when in the low change treatment, birds chose the previously rewarded stimulus rather than the most recently rewarded correct stimulus, and they only did this after 24 hrs of waiting. However this difference at the 24 h retention interval is not quite significant at the 5% level ($F_{(1,7)} = 3.91$, $P = 0.088$). The shift between 1 and 24 hrs is not statistically significant for either treatment (low change: $F_{(1,7)} = 4.2$, $P = 0.0796$; high change $F_{(1,7)} = 4.16$, $P = 0.0807$).

Discussion

Summary of results

We manipulated environmental change, and asked whether this manipulation influenced our subject’s acquisition and retention of information. Our model of our experimental scenario predicts that the value of memories should decrease with the passage of time, and that as change increases, then initial value of the memory decreases. Our experimental results show that environmental change influences both how animals track their environment and how they later use and remember this information. Broadly speaking our subjects tracked their environments more closely in high change treatments, because they responded to changes more quickly after experiencing high rates of change. In addition, we found that change influenced how our subjects retained information in two key ways. First, after experiencing high change subjects favored past information over recent experience at short retention intervals. Second, our results show an overnight effect on memory that depends on experienced environmental change. In high change treatments, subjects showed a dramatic increase in the accuracy with which they followed their most recent experience at 24 h, while the same subjects show little effect of 24 h upon their use of recent versus past in low change treatments.

Plan of the discussion

Our discussion proceeds in three parts. First, we develop connections to and implications for the tracking models of behavioral ecology that provided the original impetus for this study. Second, we describe some important connections to animal psychology, and finally, we present some ideas about how this study combines behavioral ecology and animal psychology and how this interdisciplinary approach might be taken further.

Connections to, and implications for behavioral ecology

The predictions of tracking models—As predicted, birds sampled more under high rates of change. We expected birds exposed to high rates of change to choose the alternate stimulus more frequently, simply because the environment was changing. And in this case, sampling the alternate versus making an error immediately following a change are

indistinguishable. However we also found a difference between the high and low change treatments when we looked at choice following the acquisition of the newly rewarding choice. When the stimulus value changed frequently, birds had more to track: they had to learn those changes and switch their behavior. Mechanistically, this could be attributed as a difference in practice: when birds were in a high change treatment, they experienced more reversals to learn. Importantly, this matches the predictions of tracking models which do not incorporate such a simple mechanism, such as the models by Stephens (1987) and Shettleworth et al (1988). While a few studies have tested the Stephens (1987) tracking model (Inman 1990; Shettleworth et al. 1988; Tamm 1987), only one tested more than a single level of environmental change. This study (Tamm 1987) agrees with our results in that Tamm's hummingbirds sampled more in more varying environments even though Tamm's experimental preparations differed from ours (Tamm's birds needed to sample a varying option to know its value, our birds could infer the values from sampling either option). Manipulating levels of change is an important step in empirically testing the theory on sampling and tracking, where change is such a crucial parameter in determining the adaptive function of both sampling and tracking.

Forgetting and the Value of Information—Environmental change is also predicted to change the value of information across time. We generally expect animals to choose according to their most recent experience, because the most recent state of the environment is the best predictor of the best action. Most memory models predict an orderly decay of accuracy with time, much like the textbook forgetting curve first described by Ebbinghaus (1885). Although the exact function may change, forgetting tends to show the same basic loss with time (e.g. White 2001, Ruben & Wentzel 1996, among many others). In modeling our specific experimental scenario we find that memories should lose value across time in a linear fashion. Our model specifically predicts that greater rates of change would lead to a faster decline in memory, because the values of those memories are lower to begin with. Our results did not follow these expectations. Rather than a simple main effect of retention interval, we found that an interaction between retention interval and the rate of change influenced choice. In our high change treatment, birds showed an improvement with increasing retention interval from 4 to 24 hours, and then showed the expected decline from 24 to 72 hours. However, in our low change treatment, birds showed a decline in performance between 4 and 24 hours, with a small improvement across longer intervals. The interaction is most dramatic at 24 hours, with both a significant difference between treatments and a significant positive increase between 4 and 24 hours when birds were under the high rate of change. In pilot studies with no change whatsoever, jays show the classic forgetting curves across increasing retention intervals, from 1 to 72 hours. The key difference with the current study is the addition of change, and of the final learning set. Finally, as with all studies of learning and memory, we face the classic learning-performance distinction. We can never know whether the observed choice of the animal reflects its “best” knowledge and it is quite possible that both contingencies are remembered and the animal is choosing between them.

Weighting the recent with the past—When we look at whether jays choose recent or past information, we see an interaction between rate of change and time. What accounts for

these striking differences in short retention intervals? The jays seem to be balancing past and recent information in some way. Devenport and colleagues, have developed and tested a model that places some weight on the long-term average, and some weight on the most recent experience (2005; 1994; 1997). The basic prediction is that animals should favor recent experience after short intervals of time, but they should follow the long-term average after longer intervals. In our study, both alternatives were the same in the long-term (that is they were correct equally often). If we look, however, at only the second (and last) morning of experiencing change, the Devenports' Temporal Weighting Rule qualitatively predicts the observed transition of choice that favors recent experience to choice favoring past experience. Quantitatively, however, the rule predicts a switch in choice much earlier than the observed transition, within dozens of trials rather than a full day of trials later. In an attempt to explain this quantitative disagreement, we investigated the possibility that jays use an alternate weighting scheme. Specifically, we looked at the cases where information that was correct at the end of the previous day conflicts with the most recently acquired information. This information was correct not only for a long period of time in hours, but was also subject to consolidation processes thought to occur during sleep (e.g. Marshall and Born 2007; Stickgold 2005; Walker and Stickgold 2004). Thus we have two alternate ways for this experience to be weighted. When recent experience conflicts with what was correct 24 hours ago, one can easily predict that the certainty of the most recent experience affects what the birds eventually choose. For instance, a bird experiencing more change within its most recent experiences might be less certain of which stimulus is correct. And that is what we found: these birds relied more on past information which had been correct during the previous night. However, in low change treatments birds followed their most recent experience after an interval of 1 hour. This preference changed after 24 hrs, when the birds switched from preferring the stimulus that was most recently correct to the stimulus that was correct during the overnight period. Birds in this case seem to be weighing information across a longer period of time: their most recent experience was relatively brief compared to the previous 5 hours of trials with a different rewarded stimulus. And across time, the choice became more evident after 24 hrs. These results are intriguing, and do seem to support the idea that birds are balancing information, rather than simply remembering only one stimulus and responding to it with an accuracy that declines with time. However, we did not design our study to explicitly test predictions of weighting past versus present experience and additional data will be required to fully explore these interactive effects.

Parallels with studies of reversal learning—In design, our experiment most closely resembles reversal learning studies performed by animal psychologists (a few classics in this vast literature are Bitterman et al. 1958; Gossette et al. 1966; Mackintosh et al. 1968). In these studies, animals faced with a sequence of reversals in reward contingency, respond to these changes more quickly as they experience repeated reversals. Psychologists commonly attribute this improvement in learning performance to what they call a 'transfer of training,' where learning one task improves learning of subsequent related tasks, because past experience transfers to the new situation (e.g. Thorndike 1911; Thorndike and Woodworth 1901). There are, however, two other possible explanations. First, animals may learn a win-stay, lose-shift strategy, and they may learn to respond to win's more quickly in high change environments. And finally, learning may simply be more difficult for the birds when change

occurs infrequently. This could happen because animals experience the same conditions over longer intervals when change occurs infrequently, and this could cause proactive interference that makes it difficult to ‘unlearn’ an earlier long-lasting condition. Our design including a final learning set (introducing a final switch for every treatment), places this study firmly within an interference learning paradigm. These well-described effects of transfer and interference are likely very biologically relevant to animals in their natural environments. This is especially true in a situation like ours, which is closer to natural situations, where subjects experience a continuous string of reversals, at often unpredictable intervals, throughout the day in a closed-economy system; as opposed to a small number of reversals per day experience over a brief experimental session.

Overnight and Circadian Effects—The most striking result of our experiment is the differences between choices bird makes under high and low change after 24 hours. This is not the first description of overnight experience affecting how experience appears to be weighted. For instance, Prabhu and Cheng (2008a) described a strict circadian effect in how honeybees applied memories of a conflicting color discrimination task, finding differences between choice at 22 h and 24 h. Here the explanation was not overnight experience, but rather an explicit circadian rhythm learned after a single day of experience (see also Pahl et al. 2007; Prabhu and Cheng 2008b; Zhang et al. 2006). We don’t test explicitly for a circadian effect, however we do find evidence for an overnight effect. Our results stand out because while we found that 24 h retention intervals are special, we also found the extent of their ‘specialness’ depends on the environmental variability a subject has experienced. After 1hr, birds in a highly changing environment ignored recent experience and more heavily relied on their overnight memories. However after 24 hrs, birds under high change tended to follow their most recent experience. In the high change treatment, changes occurred every 60 minutes on average. So after any period of two or more hours, the best strategy is to choose randomly because prior experience no longer predicts the state of the environment. The birds, however, did not choose randomly, instead observed choice behavior interacted with retention interval. A possible explanation is that in a variable world, subjects will choose the stronger stimulus memory, thus for short retention intervals, the birds under high change relied on experience of what was correct overnight. However, unlike birds in the low change treatment, the birds in the high change treatment did not disregard the most recent information when it came to 24 hr intervals: this information presumably gained more strength as time progressed, and another overnight interval occurred.

Lessons for the integration of behavioral ecology and cognition

Our study was inspired by tracking models from behavioral ecology, and we can reasonably interpret much of what we’ve found in light of the basic models. Our most intriguing finding is, however, mechanistic. We find that 24 h retention intervals have significant properties. Mechanistically this is not surprising, the daily cycle is incredibly important for all earth bound organisms, and prior evidence support the special properties of circadian cycles (e.g. Decker et al. 2007; Lehmann et al. 2011; Refinetti 2005), as well as the overnight effects of sleep in both timing and memory (e.g. Diekelmann and Born 2010; Gerstner et al. 2009; Rawashdeh et al. 2007). What is surprising and novel, however, is that the specialness of the 24 h retention interval depended on environmental change, a variable we manipulated

because of its importance in tracking models. This suggests, we argue, some important opportunities to develop connections between the adaptationist models of behavioral ecology and more mechanistic constraints from animal psychology and timing. For instance, how do consolidation processes or the presence of information as working memories or reference memories affect how experiences are weighted in future decisions? Our results suggest that change affects the weighting of information dependent upon a two compartment version of stored information, akin to working memory and reference memory. Thus tracking might differ at circadian scales versus ‘interval’ scales of single foraging bouts, like that traditionally modeled. This connection between ‘tracking’ and circadian intervals suggests that environmental features that vary on different time scales may shape the evolution of biological clocks and their periodicities.

Summary

Many studies show that change affects how animals acquire and use information: e.g. how frequently the sample, and how quickly they learn about new states of environment. Our blue jays followed these basic predictions by sampling more and learning more quickly when environment changed more frequently. Our study also asked how different regimes of environmental change affect the retention and use of information following the passage of time. Theory predicts that the value of remembered information should steadily degrade as time passes, our results do not support this simple claim. Our subjects were clearly balancing their most recently acquired information with their past information, and environmental change influenced how the jays struck this balance. The passage of time, and specifically overnight events, interact with choice and affects the weighting of old information versus what have been most recently acquired. An intriguing avenue of further research would be to design a study to test these interactions more explicitly. We have identified a pattern, but have only tested two extremes of change. A next step in investigating how overnight events interact with change would be to manipulate these reward ratios, such that one stimulus is more correct on average, either across all experience or at different periods of time. This study adds to the increasing body of literature investigating how information is integrated and then often applied differently depending on the time scale between experience and later decision.

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References

- Anderson JR, Schooler LJ. Reflections of the environment in memory. *Psychological Science*. 1991; 2:396–408.
- Bitterman ME, Wodinsky J, Candland DK. Some comparative psychology. *American Journal of Psychology*. 1958; 71:94–110. [PubMed: 13521022]

- Daan S. Learning and Circadian Behavior. *Journal of Biological Rhythms*. 2000; 15:296–299. [PubMed: 10942260]
- Decker S, McConaughy S, Page TL. Circadian regulation of insect olfactory learning. *Proceedings of the National Academy of Sciences*. 2007; 104:15905–15910.
- Devenport JA, Patterson MR, Devenport LD. Dynamic averaging and foraging decisions in horses (*Equus caballus*). *Journal of Comparative Psychology*. 2005; 119:352–358. [PubMed: 16131264]
- Devenport LD, Devenport JA. Time-dependent averaging of foraging information in least chipmunks and golden-mantled ground squirrels. *Animal Behaviour*. 1994; 47:787–802.
- Devenport LD, Hill T, Wilson M, Ogden E. Tracking and averaging in variable environments: a transition rule. *Journal of Experimental Psychology: Animal Behavior Processes*. 1997; 23:450–460.
- Diekelmann S, Born J. The memory function of sleep. *Nature Reviews Neuroscience*. 2010; 11:114–126.
- Dunlap AS, McLinn CM, McCormick H, Scott M, Kerr B. Why some memories do not last a lifetime: optimal long-term recall in changing environments. *Behavioral Ecology*. 2009;20.
- Gerstner JR, Lyons LC, Wright KP, Loh DH, Rawashdeh O, Eckel-Mahan KL, Roman GW. Cycling Behavior and Memory Formation. *Journal of Neuroscience*. 2009; 29:12824–12830. [PubMed: 19828795]
- Gossette RL, Gossette MF, Riddell W. Comparisons of successive discrimination reversal performances among closely and remotely related avian. *Animal Behaviour*. 1966; 14:560–564. [PubMed: 5972814]
- Harley CB. Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*. 1981; 89:611–633. [PubMed: 7289638]
- Houston, AI.; Kacelnik, A.; McNamara, JM. Some learning rules for acquiring information. In: McFarland, D., editor. *Functional ontogeny*. Boston: Pitman; 1982. p. 140-191.
- Inman, A. Foraging decisions: the effects of conspecifics and environmental stochasticity. Oxford University; 1990. Ph.D. dissertation thesis
- Killeen, PR. Averaging theory. In: Bradshaw, CM.; Szabodi, E.; Lowe, CF., editors. *Quantification of steady-state operant behavior*. Amsterdam: Elsevier; 1981. p. 21-34.
- Lehmann M, Gustav D, Galizia CG. The early bee catches the flower – circadian rhythmicity influences learning performance in honey bees, *Apis mellifera*. *Behavioral Ecology and Sociobiology*. 2011; 65:205–215. [PubMed: 21350590]
- Mackintosh NJ, McGonigle B, Holgate V. Factors underlying improvement in serial reversal learning. *Canadian Journal of Psychology*. 1968; 22:85–95. [PubMed: 5649040]
- Mangel M. Dynamic information in uncertain and changing worlds. *Journal of Theoretical Biology*. 1990; 146:317–332. [PubMed: 2259206]
- Marshall L, Born J. The contribution of sleep to hippocampus-dependent memory consolidation. *Trends in Cognitive Sciences*. 2007; 11:442–450. [PubMed: 17905642]
- McNamara JM, Houston AI. Optimal foraging and learning. *Journal of Theoretical Biology*. 1985; 117:231–249.
- McNamara JM, Houston AI. Memory and the efficient use of information. *Journal of Theoretical Biology*. 1987; 125:385–395. [PubMed: 3657218]
- Pahl M, Zhu H, Tautz J, Zhang SW. Circadian times episodic-like memory-- a bee knows what to do, and also where. *Journal of Experimental Biology*. 2007; 210:3559–3567. [PubMed: 17921157]
- Prabhu C, Cheng K. One day is all it takes: circadian modulation of the retrieval of colour memories in honeybees. *Behavioral Ecology and Sociobiology*. 2008a; 63:11–22.
- Prabhu C, Cheng K. Recency preference of odour memory retrieval in honeybees. *Behavioral Ecology and Sociobiology*. 2008b; 63:23–32.
- Rawashdeh O, de Borsetti NH, Roman G, Cahill GM. Melatonin Suppresses Nighttime Memory Formation in Zebrafish. *Science*. 2007; 318:1144–1146. [PubMed: 18006748]
- Refinetti, R. *Circadian Physiology*. Boca Raton: CRC Press; 2005.
- Shettleworth SJ, Krebs JR, Stephens DW, Gibbon J. Tracking a fluctuating environment: a study of sampling. *Animal Behaviour*. 1988; 36:87–105.

- Stephens, DW. Models of information use. In: Stephens, DW.; Brown, JS.; Ydenberg, RC., editors. Foraging: Behavior and Ecology. Chicago: The University of Chicago Press; 2007. p. 31-60.
- Stephens, DW.; Dunlap, AS. Foraging. In: Menzel, R., editor. Learning and Memory: A Comprehensive Reference. Oxford: Elsevier; 2008. p. 365-384.
- Stickgold R. Sleep-dependent memory consolidation. *Nature*. 2005; 437:1272–1278. [PubMed: 16251952]
- Tamm S. Tracking varying environments: sampling by hummingbirds. *Animal Behaviour*. 1987; 35:1725–1734.
- Thorndike, EL. *Animal Intelligence*. Darien, CN: Hafner; 1911.
- Thorndike EL, Woodworth RS. The influence of improvement in one mental function upon the efficiency of other functions. *Psychological Review*. 1901; 8:247–261. 384–395, 553–564.
- Valone TJ. Are animals capable of Bayesian updating? An empirical review. *Oikos*. 2006; 112:252–259.
- Walker MP, Stickgold R. Sleep-Dependent Learning and Memory Consolidation. *Neuron*. 2004; 44:121–133. [PubMed: 15450165]
- Zhang SW, Schwarz S, Pahl M, Zhu H, Tautz J. Honeybee memory: a honeybee knows what to do and when. *Journal of Experimental Biology*. 2006; 209:4420–4428. [PubMed: 17079712]

Highlights

- > We describe a model and experiment applying basic tracking theory in foraging to an operant learning paradigm.
- > Blue jays perform as expected with their basic sampling and tracking behavior.
- > We explore the hypothesis that memory length should be tied to the value of information learned and that environmental change is a key determinant of the value of memory.
- > We found an interaction between the rate of environmental change and the passage of time, likely influencing how birds balance recent and past information.

Figure 1.

The effect of increasing change (lower values of q) is to depress the value of memory. Because dynamic optimization works backwards, the highest points of each graph at time step 25, indicates the initial value of memory following experience. The value of memory then declines as time steps proceed towards the end.

Figure 2.

Results for $q=0.98186$ and $\varepsilon=0.01$. We chose the q value based upon the rate of change in the experiment in this paper. In 2b, the sharpest V-shape represents the beginning time step, with each of the next time steps following in order with more and more shallow V-shapes.

Figure 3.
The experimental apparatus.

Figure 4.

Design of the experimental trials. Birds experience variability in the form of stimulus reward reversals. In the low change treatment, birds experience stimulus A correct for five hours, then stimulus B is correct for the next five elapsed hours of trials. In the high change treatment, stimulus A and B reverse reward on average every 60 min. The correct stimulus overnight could be either stimulus A or B depending on when the reversals occurred. During the morning of Day 2, the rewarding stimulus reverses for a final time in both treatments. The value then remains stable until the bird reaches a criterion of accuracy. We call this period the final learning set, since this comprises the experience we then test the birds' later choices against. Birds then begin a simple task following white lights, into which we insert a single probe trial following the predetermined interval of time.

Figure 5.

The mean performance of birds when making choices relative to the last stimulus they experienced as correct, over five retention intervals. Birds were exposed to different rates of environmental change (low or high), and tested at each interval in a within-subjects design. The bars reflect the standard deviations.

Figure 6.

The deviation from expected for birds choosing according to the stimulus that was correct after the first day of learning, when that stimulus conflicted with the most recently correct stimulus. Values above zero on the Y-axis tend towards choosing the overnight stimulus (past information) more than expected by chance, while negative values are moving towards choosing the most recently-rewarded stimulus (recent information) more than expected by chance.

Table 1

Possible outcomes concerning the state variable.

Event	Probability
A true and A recognized	$p(1 - \varepsilon)$
A true and B recognized	$p\varepsilon$
B true and A recognized	$(1 - p)\varepsilon$
B true and B recognized	$(1 - p)(1 - \varepsilon)$

Table 2

Events observable by the subject.

Event	Probability
A recognized	$p(1 - \varepsilon) + (1 - p)\varepsilon$
B recognized	$p\varepsilon + (1 - p)(1 - \varepsilon)$