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Using the past to anticipate the future in human foraging behavior



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ARTICLE INFO

Article history: Received 30 October 2014 Received in revised form 26 March 2015 Available online 11 April 2015

Keywords: Human foraging Optimal foraging Temporal structure History effect Context effect Visual search

ABSTRACT

Humans engage in many tasks that involve gathering multiple targets from their environment (e.g., picking berries from a patch). Such foraging tasks raise questions about how observers maximize target collection – e.g., how long should one spend at one berry patch before moving to the next patch. Classic optimal foraging theories propose a simple decision rule: People move on when current intake drops below the average rate. Previous studies of foraging often assume this average is fixed and predict no strong relationship between the contents of the immediately preceding patch or patches and the current patch. In contrast to this prediction, we found evidence of temporal effects in a laboratory analog of a berry-picking task. Observers stayed longer when previous patches were better. This result is the opposite of what would be predicted by a model in which the assessment of the average rate is biased in favor of recent patches. This result was found when patch quality varied systematically over the course of the experiment (Experiment 1). Smaller effects were seen when patch quality was randomized (Experiment 2). Together, these results suggest that optimal foraging theories must account for the recent history to explain current behavior.

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1. Introduction

Humans, like other animals, engage in foraging tasks in which they must gather multiple, indeterminate numbers of targets from a 'patch' of stimuli before moving along to the next patch. Like animals, this foraging could involve acquisition of resources like food: How many berries should you pick from this patch before moving to the next (Wolfe, 2013)? How long should you wait for a bite at this fishing hole (Hutchinson, Wilke, & Todd, 2008)? In addition, the principles of foraging extend to our mental life: How long should you 'fish' for a word in the pool of your long-term memory (Wilke et al., 2009)? Moreover, civilization creates new foraging tasks: How long would you stay on one webpage before moving to another (Pirolli, 2007; Pirolli & Card, 1999)? How long should a radiologist search in an X-ray image to find tumors?

In these types of tasks, people are faced with the decision of when to quit searching and move to the next patch? One possible solution is to search exhaustively, to leave when all the targets are

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found. But individuals rarely do this. People leave berry patches even though some perfectly adequate berries remain (Wolfe, 2013). Similar results have also been found in animals (e.g., Cowie, 1977). Search termination in foraging tasks has been extensively studied in the animal foraging literature (Oaten, 1977; Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986). Much of this works takes as a starting point Charnov's work on Optimal Foraging (Charnov, 1976; Pyke, Pulliam, & Charnov, 1977), specifically, his Marginal Value Theorem (MVT) that holds that animals attempt to maximize their intake and that this can be accomplished by leaving the current patch when current intake drops below the overall average intake.

These models of animal foraging have been successfully applied to work with humans. In Wolfe's (Wolfe, 2013) computerized version of a berry-picking task, human foragers followed the predictions of MVT in a world of roughly identical patches, at least, when data are averaged over observers. And a Bayesian relative of MVT has been applied to study visual search for T-shaped targets among pseudo-L-shaped distracters (Cain et al., 2012).

In lab-based studies of foraging, it is often assumed that the forager knows the average yield from the task over time and that this average is of more-or-less fixed quantity. These assumptions need not hold. For instance, when Hutchinson, Wilke, and Todd (2008)

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had observers 'fishing' in a succession of fishing holes. Greater success in the previous location seemed to shorten the amount of time an observer was willing to spend in the current location. This suggests that patch leaving time can be modulated by recent information.

Hutchinson's fishing holes varied randomly in quality. However, the real world can have temporal structure in which events close in time are likely to be similar but where the nature of those events can change over time. Dependence on orderly prior history has been explored in a variety of human perception literatures. For instance, classic ambiguous figures like the duck-rabbit, popularized by Jastrow (1899) or the young girl – old lady (Boring, 1930) are subject to hysteresis effects. If you see an unambiguous duck morph into the duck-rabbit, the ambiguous case will be more likely to be seen as 'duck' than if an unambiguous rabbit is the starting place. See Fig. S1 of Kietzmann, Geuter, and Kong (2011) for a good collection of such stimuli.

In the present paper, we explored the effects of a consistent gradual change in target density on observers' behavior in a simple foraging task, modeled on berry picking as in Wolfe (2013), where small red squares in a patch were used to represent "berries" while green squares were "leaves" (see Fig. 1 for two examples of stimuli configuration). In Experiment 1, we asked observers to pick berries in as little time as possible. Historical dependencies were introduced by modulating between periods of high and low target density over the course of the study. This allowed us to compare foraging behavior during rising and falling phases. To anticipate our results, we found that Marginal Value Theorem (MVT) gave a good account of average behavior. Beyond that, there are systematic effects of the modulation of patch quality. Observers foraged longer in a patch, producing more hits and more false alarms, when patch quality was falling than when it was rising. Note that this is opposite to the effect that would be predicted if "overall average rate" was replaced with the "overall average rate for the last few patches" in the usual MVT calculation. Since the average rate for the last few patches will be higher in falling than rising phases, the average of the recent patches would predict that people would guit foraging guicker in falling patches because the observed rate would drop below the average rate faster.

We also explored how much "history" information is needed for this effect. Can one single experience (one patch) produce history effects on this foraging task as it does in the fishing hole paradigm mentioned above? To answer this question, in Experiment 2, the berry patch quality changed randomly and we examined the behavior on the current patch as a function of the quality of the prior patch. Interestingly, we found that the influence of past experience still exists. Thus, for instance, even if only the immediately prior patch was of higher quality, the observers become more liberal.

2. General methods

In two experiments, we employ a simple simulated berry-picking task to explore the history effect on human foraging behavior. In each experiment, berries were presented in one of two visual conditions: Color Cue condition and No-color Cue condition. As will be discussed later, the Color Cue condition is designed to behave, on average, in accordance with the predictions of optimal foraging theory. The No-color condition is designed to violate the assumptions of the MVT. Both conditions are run in order to determine the generality of any effects of history.

The experiments were run at the Harvard Decision Science Lab. The stimuli were presented on Dell computers running Window 7. The experiments were run using the Psychophysics Toolbox version 3.0.9 in MATLAB 7.10.0 (R2010a). Each computer was connected to a 19-in. Viewsonic NX1932w monitor, whose resolution was 1440 by 900 pixels.

2.1. Stimulus material

Fig. 1 shows screenshots of the schematic "berry patches" used in these experiments. Each patch consisted of twenty by twenty squares of red or green squares. Each patch subtended 15.6 degree of visual angle and a square subtended 0.8 degree of visual angle at a 60 cm viewing distance. Observers' head positions were not constrained so it is likely that actual viewing distance varied somewhat. Observers were told that green squares were "leaves" and were to be ignored. The color of green squares varied in RGB color space from [0,51,0] to [0,100,0] with uniform distribution of green color channel. Forty of the squares (10%) were red shaded "berries". The red shaded berries could be good or bad. Good berries were worth 5 points. Bad berries cost 1 point. The number of "good" berries (patch quality) varied between 8 and 32 among 40 (20% and 80% targets).

In the Color Cue condition, berries differed in color (Fig. 1A) and the differences in color were partially correlated with whether the berries were good or bad. Berry colors were defined in RGB color space by the triplet [R, (255-R)/2, (255-R)/2], where R stands for

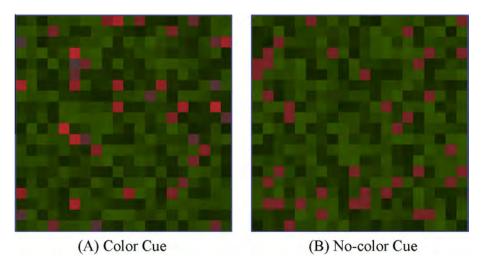


Fig. 1. Stimulus configuration: modified screenshot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the value of red color channel. R for good berries had a mean of 220 and a standard deviation of 32. R for bad berries had a mean of 140 and a standard deviation of 32. Thus the d' of the color signal was 2.5. This made the color of a berry an informative but imperfect guide to its 'goodness'. Observers were instructed that brighter redder berries were more likely to be good berries than the darker berries, but that color information was not completely reliable. In the No-color Cue condition (Fig. 1B), all berries had the same redness ([180,38,38]). Observers learned if a berry was good or bad only after it was picked.

Once a berry was picked it was replaced by green square. Points were visible onscreen at the upper right corner without overlap with the berry patch and updated after each pick. Observers were informed as to whether a berry was good or bad by auditory feedback. A low pitch tone (650 Hz) indicated a good berry and higher pitch tone (850 Hz) indicated a bad berry.

2.2. Procedure

The procedure of all experiments followed the paradigm shown in Fig. 2. The experiment consisted of a series of patches in which observers foraged for good berries. Within each patch, observers selected berries by moving and clicking on a red square in the display. Click time for each berry is self-paced. Clicked berries disappeared. Observers earned 5 points for a good berry or lost 1 point for a bad berry. The total score which was located in the upper right corner of the screen was automatically updated after each click. Observers could click any number of berries in a display and were allowed to leave the patch at any time. Observers moved to the next patch by clicking on the "next patch" box which was located in the lower right corner of the screen. After a 3s delay, a new display would be presented.

Observers completed one Color Cue session and one No-color Cue session. Some observers did Color Cue session first and then No-color Cue session while others did the experiment with a flipped order. To complete a session, observers needed to reach a total of 3000 (Color Cue) or 2000 (No-color Cue) points. Observers were asked to collect more points in the Color Cue condition because the color of each berry makes it easier to pick good berries. The two point goals roughly equated the time required to

complete the two sessions of the experiment. Since the point threshold determined the termination time of the study, observers were motivated to collect points as quickly as possible.

3. Experiment 1

3.1. Specific methods

Patch quality varied from 20% to 80% (8–32 good berries out of 40 berries) and each step changed the percentage of good berries by 10%. In Experiment 1, quality was structured, meaning that it varied with one of two temporal orders during a session. Observers were assigned into a "rising–falling" or "falling–rising" pattern (Fig. 3). The temporal structures were designed to provide systematic, historical information to subjects. Although observers were not informed about temporal structures, they could learn the structures over the course of the experiment.

A total of twenty-four observers took part in this experiment. Fourteen observers were tested (seven males), mean age 30 (18–52 years old) with rising–falling patch quality pattern. Ten observers were tested (five males), mean age 32 (18–52 years old) for falling–rising patch quality pattern. In the absence of an obvious way to perform a power calculation (i.e. unknown effect size), we used a relatively large number of observers. Given that Wolfe (2013) used 10 observers for the basic version of a foraging experiment, we used $2.4\times$ that number to look for a modulation of that basic foraging behavior. All observers gave informed consent approved by Brigham and Women's Hospital and consistent with the Declaration of Helsinki. All were paid \$10/h for their time. All had vision corrected to at least 20/25 and passed the Ishihara color vision screen.

3.2. Results

Since we are interested in the effect of temporal structure on observers' foraging behavior, it is important that observers should be exposed to that structure. Therefore, we eliminated the data of the observers who ended the experiment before experiencing at least one full cycle of patches (24 patches). Two observers' data

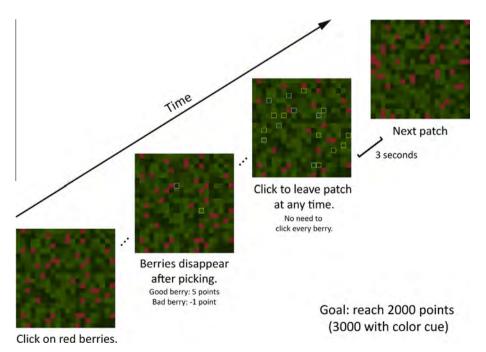


Fig. 2. The procedure of the experiment.

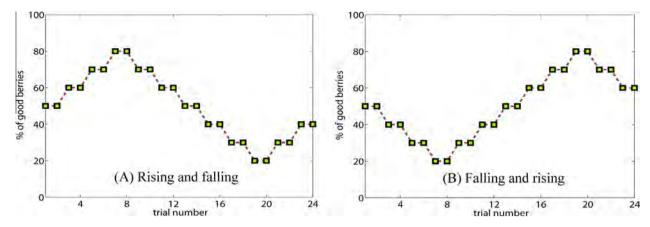


Fig. 3. Patch quality pattern with temporal structure. The *X*-axis represents the trial number. Each circle of the temporal structure has 24 trials. There are an unlimited number of patches that observers could exploit. The *Y*-axis indicates the percentage of good berries in one trial (one berry patch).

were removed because of this. It is also important that the observers foraged in a meaningful manner. Os who picked every berry in every patch or who picked very few berries in every patch produce data that cannot be analyzed for changes in foraging behavior. Thus, we eliminated observers who picked more than 90% (36 among 40) berries in more than 75% patches or less than 10% (4 among 40) berries in more than 75% patches. Because of this, four observers' data were removed. By these rules, totally six observers' data were eliminated from analysis (three from the rising–falling pattern and three from the falling–rising pattern). In fact, the basic pattern of results, described below, holds whether or not these observers are excluded.

Three metrics were examined in this experiment: average number of berries picked in a patch, the percentage of good berries picked (pHit), and the percentage of bad berries picked (pFA) in order to assess observers' foraging behavior.

3.2.1. Comparing the two temporal orders

Since two structured patch quality patterns (rising–falling and falling–rising) were employed in this experiment, we first analyzed whether there was a significant difference in observers' overall foraging behavior between as a function of temporal structure. T-test analyses revealed no significant differences between the two temporal structures in any of the three metrics (number of berries picked: t(16) = 0.1721, p = 0.8655; pHit: t(16) = 0.05818, p = 0.9543; pFA: t(16) = 0.3917, p = 0.7004). For subsequent analyses we combined data from the temporal conditions.

3.2.2. Average responses are consistent with the MVT

In a uniform world, an optimal forager will leave the current patch/location when the current intake rate (instantaneous rate)

is lower than average intake rate (overall rate). Although previous researchers (e.g., Wolfe, 2013) have found that average human foraging behavior follows this rule in a world of roughly uniform patches, we did not know how observers' foraging behavior would change in our temporally structured world. Results of this analysis are shown in Fig. 4. For each observer, we compute different instantaneous rates for different clicks. To compute the instantaneous rate, data from multiple patches of one observer are aligned to the last selection of each patch. That is, we average time and performance for the last selection, the penultimate selection, and so on, backwards in time. The last selection is plotted at its average position in the sequence of selections. That is, if an observer ended foraging after 18, 20, and 22 selections, the last click data would be plotted the average position, 20, the penultimate selection, at 19, and so on. For each position, a Positive Predictive Value (PPV) is defined as (good berries)/(total berries picked) at each position. In the Color Cue condition, PPV will tend to fall over time in a patch because good berries are initially easy to find and become scarcer over time. In the No-color Cue condition, this dependency is not seen. The 10th clicked berry is just as likely to be as good as the 1st clicked berry because observers have no information about berry quality. Instantaneous rate is computed as PPV/(average time for that position as click speed). Note that this is an average "instantaneous rate". In this experiment, the term does not have much meaning for a single response. For each observer, we also get an overall rate. Overall rate is calculated by the total score of this observer divided by total elapsed time spent in the experiment (including the 3 s "travel time" between patches when no berries can be collected).

Fig. 4A shows the instantaneous rate of last ten clicks in both falling and rising periods and the overall rate with color cue.

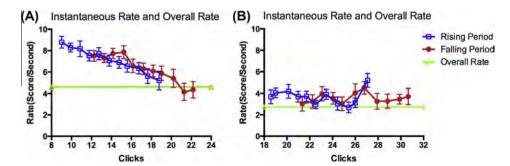


Fig. 4. Instantaneous rate of last ten clicks for rising (blue) and falling (red) periods in the Color Cue condition (A) and the No-color Cue condition (B). Horizontal green lines show the overall rate. Each error bar represents standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 4B shows the same data for the No-color Cue Condition. We compare the instantaneous rates of last clicks to the overall rate using *t*-tests in order to see if foraging behavior is modulated by the temporally structured world.

Fig. 4A shows that the instantaneous rate falls as it gets harder to find a good berry and the rate for the final selection in the patch is close to the average rate for the task. From the *t*-test, we can see that there is no significant difference between the instantaneous rate of the last click and the overall rate in either the rising period (t(17) = 0.7256, p = 0.4780) or the falling period (t(17) = 0.3529,p = 0.7285) of the temporal structure. Working backwards in time, instantaneous rate and overall rate becomes significant at two clicks before the final click in the rising period (t(17) = 3.304,p = 0.0042); and is highly significant at three clicks (t(17) = 3.593, p = 0.0011). Similarly, instantaneous rate and overall rate become significantly different at three clicks before the final click in the falling period (t(17) = 2.112, p = 0.0498); and is highly significant at four clicks (t(17) = 2.682, p = 0.0079). These tests suggest that MVT makes a reasonable prediction about human foraging behaviors in both rising and falling periods.

Fig. 4B shows the instantaneous rate for the last ten clicks in both falling and rising periods without the color cue. In the absence of visual information about berry quality, the instantaneous rate of different clicks is relatively stable but tends to rise at the end of the sequence of selections. Seemingly, observers like to leave patches of this sort having collected just one more good berry. In the absence of a color cue, observers are not quitting when the instantaneous rate approaches the overall rate (see also Wolfe, 2013).

3.2.3. How does an orderly past history influence foraging behavior?

Of most relevance for the present work, we compared our foraging metrics for rising and falling phases to determine if recent past history influences foraging behavior. We limited our analyses to median quality patches (50% targets) and the patches above (60%) and below (40%) because historical dependence would be strong (multiple preceding patches were consistently rising or falling). With more extreme patches, there has been a recent transition from rising to falling or vice versa. For example, a 30% is preceded by a 20% patch (rising), but this patch is preceded by a 30% patch (falling). Importantly, average patch quality is equivalent between rising and falling periods and the same specific patch qualities are seen under rising and falling conditions.

3.2.3.1. Number of berries picked. Fig. 5 shows the number of berries picked from each patch in the rising and falling periods for Color Cue and No-color Cue conditions. A two-way ANOVA with temporal condition (rising/falling) and color condition (Color Cue/No-color Cue) as factors revealed strong rising/falling differences for both conditions. Observers picked significantly more berries in falling

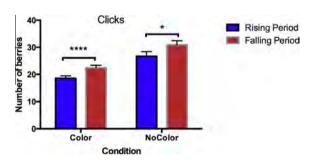


Fig. 5. Number of berries picked in each patch as a function of rising vs falling temporal structure and color vs No-color Cue Conditions. Each error bar represents the standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

period patches (F(1, 17) = 27.61, p < 0.0001). Observers also picked significantly more berries in the No-color Cue condition than in the Color Cue condition (F(1, 17) = 62.79, p < 0.0001).

T-tests show a highly significant history effect in the Color Cue (t(17) = 5.142, p < 0.0001) and a significant history effect in the Nocolor Cue condition (t(17) = 2.588, p = 0.0191). The interaction of rising/falling with condition was not significant (F(1, 17) = 0.02691, p = 0.8716). However, this is a null result and the experiment may not have had enough power to detect a difference. Further work would be needed to determine whether cues about the value of an item, available before picking, modify temporal effects.

3.2.3.2. pHit and pFA. We analyzed the percentage of good berries (pHit) and bad berries (pFA) picked from each patch in the rising and falling periods for both Color Cue and No-color Cue condition (Fig. 6) using separate two-way ANOVAs with recent history (rising/falling) and color condition (Color Cue/No-color Cue) as factors. Both ANOVAs revealed strong effects of recent history and color condition. Observers picked more good berries and more bad berries in falling period patches (pHit: F(1, 17) = 19.76, p = 0.0004; pFA: F(1, 17) = 33.05, p < 0.0001). And observers picked more good berries and more bad berries in the No-color Cue condition than in the Color Cue condition (pHit: F(1, 17) = 25.09, p = 0.0001; pFA: F(1, 17) = 358.9, p < 0.0001). Similar to the results for number of berries picked, there was no significant interaction between recent history and color condition (pHit: F(1, 17) = 0.2228, p = 0.6479; pFA: F(1, 17) = 0.01378, p = 0.9079).

3.2.4. Does the history effect accumulate?

Returning to Fig. 3, we can see that the 80% and 20% patches occur in two different environments. The experiment began at 50% patch quality and either increased to 80% (rising-falling) or decreased to 20% (falling-rising). In rising-falling version, the 80% patches are preceded by a relatively short rising run and the 20% patches are preceded by a long falling run. In the falling-rising version, the situation is reversed. The 80% patches are preceded by long rising run and the 20% patches are preceded by a short falling run. If the history effect accumulated, one might expect the longer runs to produce more dramatic effects than the shorter ones. In fact, t-test analyses revealed that there is no difference between behavior in the 20% patch after long falling runs and short falling runs (Color Cue condition: p = 0.4834; No-color Cue condition: p = 0.4604). Nor was there any difference between behavior in the 80% patch after long rising runs and short rising runs (Color Cue condition: p = 0.9370; No-color Cue condition: p = 0.5913). Of course, this is a null effect and accumulation might be seen in an experiment that had more power. However, as will also be seen in Experiment 2, it seems more likely that history effects plateau fairly quickly.

3.3. Discussion

Experiment One explored human foraging behavior when there were orderly changes in patch quality over time. We found that MVT did a good job of explaining observers' overall foraging behavior in the Color Cue condition. The number of berries picked per patch was well predicted by an MVT analysis on instantaneous rate. Beyond the average behavior, we observed systematic changes in foraging behavior between rising and falling phases. Observers were foraging longer during falling than rising phases. This is the opposite of what would be predicted if we assumed that the MVT estimate of the average rate was based on the last few patches. The average rate, especially, the recent average, will be higher during falling than rising phases (since there were more targets in the past during falling phases) and therefore recent

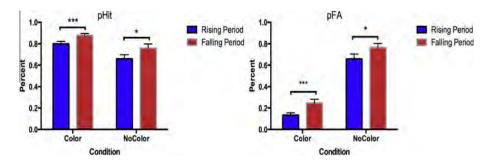


Fig. 6. The percentage of good berries and false alarms picked in each patch with temporal structure. Error bars represent standard error of the mean.

averaging would suggest that people should leave sooner during falling phases because the current rate will drop below the average rate faster. Why do observers forage longer during falling phases? There are two possible reasons. One is that history changes observers' predictions about the current patch. If that last patch was good, then the current patch should be similarly good. The opposite logic would hold when patch quality is rising. Now observers would underestimate the current quality of the patch and be inclined to give up on the patch sooner. Another possible reason would be that the direction of recent experience changes observers' prediction about the rate in the short-term future. During the falling period, the observers might have the same assessment of the current patch as they would have in the rising period. However, in the falling period they might infer that the next patch will be worse and, thus, they should stay in the current patch a bit longer. In the rising period, the next patch will be better, so it might be wise to move there sooner. Experiment 1 cannot discriminate between these two accounts. As we will see, Experiment 2 provides modest evidence in favor of the first of these two hypotheses.

MVT calculations were not useful in No-color Cue condition (also see Wolfe, 2013). MVT assumes that the instantaneous rate will decline as the resource is depleted. With an easy search and no information distinguishing "good" berries from "bad" berries, observers simply collect points at a roughly steady rate until they decide to leave the patch. There is no decline in the instantaneous rate of return (see Fig. 4) so observers must use some other rule to decide when to quit. In Experiment 6 of Wolfe (Wolfe, 2013), observers seemed to probability match (on average) in this condition. That is, on average, they would pick about 30% of all berries, good and bad, in a 0.3 quality patch, 40% in a 0.4 patch and so forth. Whatever the quitting rule in this condition, observers still showed a history effect. Just as in the Color Cue Condition, observers stay longer when patches are falling in quality. In the No-color Cue Condition, observers can create an estimate of patch quality from the feedback received each time they pick a berry. For patches of middle quality (0.4-0.6), observers collect less positive feedback in the rising phase than in the falling phase. The two hypotheses, noted above, could be at work here, too. Either observers think that the same, current patch is better in a falling context than in a rising context or, in the falling phase, they think that they next patch will be worse and, thus, stay a bit longer in the current patch.

4. Experiment 2

In Experiment 1, patch quality varied in a systematic manner over many patches. From that experiment, we can see in temporally structured environments, recent experience influences human foraging behavior. However, how much 'history' is needed to produce this history effect? To test this question, in Experiment 2, we scrambled the order of those patches. Observers saw the same patches over the course of each experiment as in Experiment 1, but in

Experiment 2, we were interested in the effect of the immediately preceding patch.

4.1. Methods

Patch quality varied randomly, as shown in the example in Fig. 7. Ten observers participated in this experiment (three males), mean age 36 (19–55 years old). All observers gave informed consent approved by Brigham and Women's Hospital and consistent with the Declaration of Helsinki. All were paid \$10/h for their time. All had vision corrected to at least 20/25 and passed the Ishihara color vision screen. Methods were the same as in Experiment 1 except that patch quality varied randomly. Observers searched until they had acquired 3000 points in Color Cue condition or 2000 points in No-color Cue condition.

4.2. Results

As in Experiment 1, we discarded the data of the observers who didn't finish a full set of 24 patches (no observers' data removed because this) or who picked more than 90% berries in more than 75% of patches or less than 10% berries in more than 75% of patches (one observer's data removed). This led to removal of only one observer's data.

In this experiment, the current patch was deemed to be a "falling" patch if the immediately preceding patch had a higher patch quality. "Rising" patches had lower quality preceding patches. As in Experiment 1, we compared these two phases in Color Cue and No-color Cue conditions; in this case, to examine if observers' visual foraging behavior was influenced by short-term history. In order to be comparable to Experiment 1, we used the data from the patches with 40%, 50% and 60% targets and excluded the data from the more extreme patches. Note that a patch with 80% targets

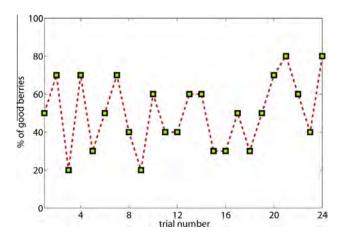


Fig. 7. Patch quality pattern with random structure.

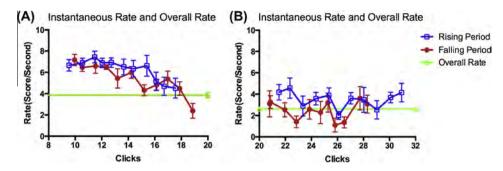


Fig. 8. Instantaneous rate for the last ten clicks for rising (blue) and falling (red) periods in the Color Cue Condition (A) and the No-color Cue Condition (B). Horizontal green lines show the overall rate. Each error bar represents the standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

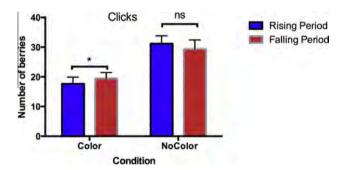


Fig. 9. Number of berries picked in rising and falling periods when patch quality varies randomly. Each error bar is the standard error of the mean.

will always be a "rising" patch because the preceding patch must be over lower quality. Similarly, a 20% patch will always be a "falling" patch. The 40–60% patches provide a mix of "rising" and "falling" cases, making the rising–falling comparisons more sensible.

4.2.1. Average responses are consistent with the MVT

Fig. 8A shows the instantaneous rate for the last ten clicks in both falling and rising periods and the overall rate in the Color Cue Condition. Fig. 8B shows the same data for the No-color Cue Condition. As in Experiment 1, we use *t*-tests to compare the instantaneous rates of last few clicks with overall rate to see if average foraging behavior follows MVT.

As shown in Fig. 8A, as the observers pick more berries, it gets harder to find a good berry. Thus, the instantaneous rate falls. In these data, the rate for the final selection in the patch is close to the average rate for the task. For the rising period there is no significant difference between the instantaneous rate of the last click and the overall rate (t(17) = 0.7728, p = 0.2309). Working backwards in time, the difference between instantaneous rate and

overall rate becomes marginally significant at two clicks before the final click (t(17) = 1.660, p = 0.0363) and more convincingly significant at three clicks (t(17) = 3.034, p = 0.0081). For the falling period, the instantaneous rate of last click is significantly lower than the overall rate (t(17) = 2.067, p = 0.0363) but is not significantly different from the overall rate at one click before the final click. Working backwards in time, instantaneous rate and overall rate becomes significant again at two clicks before the final click (t(17) = 2.408, p = 0.0213) and at three clicks (t(17) = 2.246, p = 0.0274). Thus, as in Experiment 1, the average foraging behavior in patches of randomly varying quality is broadly consistent with MVT. The pattern appears somewhat noisier than Experiment 1, though it should be noted that there are fewer observers in Experiment 2.

Fig. 8B shows the instantaneous rate for the last ten clicks in both falling and rising periods without the color cue. As in the first experiment, in the absence of visual information about patch quality, the instantaneous rate of different clicks is relatively stable but tends to rise at the end of the sequence of selections.

4.2.2. History effects

4.2.2.1. Number of berries clicked. Fig. 9 shows the number of berries picked from each rising or falling patch for Color Cue and No-color Cue conditions. There is some evidence for an effect of the preceding patch on the number of berries picked in the current patch. A difference is found between the rising and falling periods in the number of berries picked in the Color Cue Condition (t(8) = 3.250, p = 0.0117). Without the color cue, the difference between the rising and falling periods is not significant (t(8) = 0.7898, p = 0.4524) and any trend is in the opposite direction.

4.2.2.2. pHit and pFA. We also compared pHit and pFA between the rising and falling periods for both Color Cue and No-color Cue conditions, as shown in Fig. 10. In the Color Cue condition, there was a

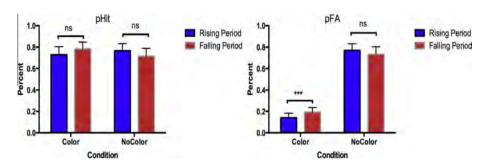


Fig. 10. The percentage of good berries (pHit) and bad berries (pFA) picked in rising and falling periods when patch quality varies randomly. Each error bar shows the standard error of the mean.

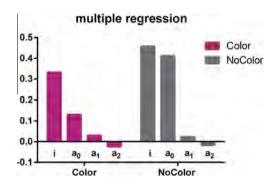


Fig. 11. The weights of different patches using multiple regression.

marginal effect of the immediately preceding patch on pHit with more berries picked in falling periods (t(8) = 2.151, p = 0.0637) and a significant effect of the immediately preceding patch on pFA with more bad berries picked in falling periods (t(8) = 5.742, p = 0.0004). Without a color cue, we found no significant effects of the immediately preceding patch on pHit or pFA (pHit: t(8) = 0.7635, p = 0.4671; pFA: t(8) = 0.7922, p = 0.4511).

4.2.3. The history effect seems to be heavily driven by the most recent trial

Since patches with different qualities are independent in this experiment, we estimate the effect of patch quality two patches back as well as one via multiple regression in this section.

Let C denote the percentage of berries picked in one patch, which is calculated as the number of clicks in this patch divided by 40 (total number of berries in each patch). Let P_0 denote the quality of current patch, P_1 denote the quality of previous patch and P_2 denote the quality two patches back. Then the percentage of berries picked in the patch C can be estimated using the following formula:

$$C = i + a_0 P_0 + a_1 P_1 + a_2 P_2 \tag{1}$$

In this formula, i is the intercept, a_0 , a_1 and a_2 are weights for P_0 , P_1 and P_2 separately. Using the data from Color Cue condition and No-color Cue condition, we can get the values of i, a_0 , a_1 and a_2 for each condition. The result is shown in Fig. 11. The intercept i estimates how many percentage of berries observer would be likely to pick without knowledge about the qualities of current patch and previous patches. From Fig. 11, we can see that the values of the intercept in Color Cue condition and No-color Cue condition are both larger than 0. Presumably this reflects some knowledge of the average patch quality. Without the knowledge of recent patch qualities, they still would pick some number of berries from current patch. Note that the intercept is larger in the No-color Cue condition than in Color Cue condition. This observation is consistent with Fig. 9 where observers pick more berries in No-color Cue condition. Comparing the weights a_0 , a_1 and a_2 for different patches, we can see that the weight of current patch a_0 is largest, the weight of previous one patch a_1 is smaller and the weight of two patches back a_2 is less than 0. Thus there is no evidence in this analysis for an effect of the 2-back patch.

4.2.4. Comparison of history effects between Experiments 1 and 2

In Experiment 2, an effect of the immediately preceding patch is found even when patch quality is randomized. Were these effects smaller than in Experiment 1? To assess this, we used two-way ANOVAs on the number of berries picked with temporal period (rising/falling) and experiment (1 or 2) as factors for both Color Cue and No-color Cue conditions. In the Color Cue condition, there is a robust main effect of temporal period (F(1, 25) = 24.69,

p < 0.0001), with people staying longer during falling phases. There was no main effect of experiment (F(1, 25) = 0.9827,p = 0.331). We found a marginally significant interaction (F(1, 1)) (25) = 3.282, p = 0.0821), driven by smaller temporal effects in Experiment 2. In the No-color Cue condition, we found no main effect of temporal period (F(1, 25) = 0.6869, p = 0.415) and no main effect of experiment (F(1, 25) = 0.3113, p = 0.5819). The interaction between these factors was significant (F(1, 25) = 4.572, p = 0.0425) reflecting smaller temporal effects in Experiment 2. Overall, the results suggest that history effects are weaker in the randomized than in the temporally structured designs. This, in turn, suggests some effects beyond those of the immediately preceding patch though the multiple regression analysis failed to detect any such effects in Experiment 2, or alternatively, that people weight prior experience more heavily when it has some predictive capacity for the future.

5. General discussion

History effects can be found in many visual tasks; for example, orientation discrimination (Fischer & Whitney, 2014) and ambiguous stimuli perception (Brascamp et al., 2008). Here we have shown that human foraging behavior, too, is influenced by recent experience. In Experiment 1, quality of patches varied systematically. Average foraging behavior was broadly consistent with MVT in the Color Cue condition. As observers picked berries from the current patch, the rate of yield from the current patch dropped. As the rate of return dropped below the average rate, observers left the patch. However, this average pattern was modulated by the temporal structure of the task. Observers foraged longer in falling than rising phases. Note, again, that the opposite effect would be predicted if the estimate of the "average rate" were biased toward the rate in recent patches. The same effect of temporal structure was found in the absence of a color cue, a condition in which MVT does not predict the patch-leaving time. It appears that the prior recent history, either changes the estimate of the current patch quality (higher in the falling than in the rising period) or it changes the prediction about the future (if quality is falling, it will continue to fall).

Experiment 2 offers some evidence in favor of the first of these hypotheses. In Experiment 2, patch quality was random over time. "Rising" and "falling" refer only to the relationship of the current patch to the preceding patch. Observers still forage longer in a current patch when the previous patch was of better quality (falling period) though this result was found only in the Color Cue condition and evidence suggested that it was weaker than in Experiment 1. Nevertheless, since the preceding patch quality does not predict the subsequent patch quality in Experiment 2, we can take this result as some evidence that observers' assessment of the current patch is influenced by the preceding patch. This evidence is, admittedly, weak and more and different data are needed on this point. In a separate series of experiments, Fougnie et al. (submitted for publication) looked at the effects of prior history on a more difficult search task. In addition, they had observers make direct estimates of the number of targets that might be present in their displays. Their results are consistent with the view that prior history changes the estimate of the current state of the world.

Acknowledgments

This research was supported by an ONR MURI (N000141010278), NIH-NEI (EY017001), Hewlett-Packard, Google, CELEST(NSF SBE-0354378) and National Natural Science Fund of China (Grant No. 61233011).

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