Separable influences of reward value on visual processing and choice

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Conflict of interest: The authors declare no competing interests.

Keywords: value-based decision making, attention, value integration, motion-induced bias, reinforcement learning

Manuscript information: 6 figures, 1 table, 2 supplementary figures, 33 pages.
Abstract 295 words
Introduction 725 words
Discussion 1333 words

Acknowledgments. We thank Vince McGinty for helpful comments on an earlier version of this manuscript. We also thank D.S. Aldrich for technical assistance. This work was supported by NIH Grant EY014924 (TM), NIH Grant DA047870 (AS), NSF EPSCoR Award #1632738 (AS), an NDSEG fellowship (RJS), and predoctoral NRSA fellowship F31MH078490 (RJS).

Abstract

Primate vision is characterized by constant, sequential processing and selection of visual targets to fixate. Although expected reward and reward value are known to influence both processing and selection of visual targets, the relationship between these effects remains unclear. Using a novel paradigm, we simultaneously measured the effects of expected reward on target selection and sensitivity to visual motion in monkeys. Monkeys freely chose between two visual targets and received a juice reward with varying probability for eye movements made to either of them. Targets were stationary apertures of drifting gratings, causing the endpoints of eye movements to these targets to be systematically biased in the direction of motion. We used this motion-induced bias as a measure of sensitivity to visual motion on each trial and utilized multiple measures to examine global and local effects of reward outcomes on choice and sensitivity to motion. Specifically, we used different reinforcement learning models to fit choice behavior and estimate reward values based on the integration of reward outcomes over multiple trials. Moreover, to compare the effects of reward value on choice and sensitivity to motion directly, we considered correlations between each of these variables and integrated reward outcomes on a wide range of timescales. We found that in addition to choice, sensitivity to visual motion was also influenced by reward value. However, choice was determined by the difference in reward values of the two options whereas sensitivity to motion was influenced by the sum of values. Moreover, models that best predicted visual processing and choice used sets of reward values based on different types of reward integration and timescales. Together, our results demonstrate separable influences of reward value on visual processing and choice, and point to the presence of multiple brain circuits for integration of reward outcomes.

Introduction

Primates make approximately 3-4 saccadic eye movements each second, and thus the choice of where to fixate next is our most frequently made decision. The next fixation location is determined in part by visual salience (Itti & Koch, 2000), but also by internal goals and reward expected from the foveated target (Markowitz, Shewcraft, Wong, & Pesaran, 2011; Navalpakkam, Koch, Rangel, & Perona, 2010; Schütz, Trommershäuser, & Gegenfurtner, 2012). Brain structures known to be involved in the control of saccadic eye movement have been extensively studied as a means of understanding the neural basis of decision-making (Glimcher, 2003; Sugrue, Corrado, & Newsome, 2005). Interestingly, the same structures also appear to contribute to the selective processing of targeted visual stimuli that tends to accompany saccades (Squire, Noudoost, Schafer, & Moore, 2013). Thus, it is conceivable that reward value controls saccadic choice and processing of targeted visual stimuli via similar mechanisms.

However, our current knowledge of how expected reward or reward value affect the processing of visual information and saccadic choice comes from separate studies using different experimental paradigms. On the one hand, the effects of reward value on saccadic choice are studied using both unequal reward outcomes (Chen & Stuphorn, 2015; Farashahi, Azab, Hayden, & Soltani, 2018; Liston & Stone, 2008; Platt & Glimcher, 1999; Strait, Blanchard, & Hayden, 2014) and dynamic reward schedules (Barraclough, Conroy, & Lee, 2004; Costa, Dal Monte, Lucas, Murray, & Averbeck, 2016; Donahue & Lee, 2015; Lau & Glimcher, 2007; Schütz et al., 2012; Sugrue, Corrado, & Newsome, 2004). On the other hand, the effects of reward value on the processing of visual information have been mainly examined using tasks with unequal reward outcomes (B. A. Anderson, 2016; B. A. Anderson, Laurent, & Yantis, 2011a, 2011b; Barbaro, Peelen, & Hickey, 2017; Della Libera & Chelazzi, 2006, 2009; Hickey, Chelazzi, & Theeuwes, 2010, 2014; Hickey & Peelen, 2017; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Rakhshan et al., 2020); but see Serences, 2008). For these reasons, the relationship between the effects of reward value on saccadic choice and processing of visual information is currently unknown.

Understanding this relationship is important because the extent to which reward influences sensory processing could impact decision making independently of the direct effects of reward on choice. For example, in controlled decision-making paradigms or natural foraging settings, recent harvest of reward following saccade or visit to certain parts of the visual field or space could enhance processing of features of the targets that appear in those parts of space, ultimately biasing choice behavior. In addition to better understanding choice behavior, elucidating the relationship between sensory processing and reward value can also be used to disambiguate neural mechanisms underlying attention and reward (Hikosaka, 2007; Maunsell, 2004, 2015), and how deficits in deployment of selective attention, which is characterized by changes in sensory processing, are affected by abnormalities in reward circuits (Volkow et al., 2009). Unfortunately, most often, the effects of reward on decision making and sensory processing are studied separately. This makes it especially difficult to discern how reward feedback is integrated to modulate choice and sensory processing, and this integration is crucial for understanding value-based choice in dynamic tasks (Bari et al., 2019; Donahue & Lee, 2015; Farashahi, Donahue, et al., 2017; Farashahi, Rowe, Aslami, Lee, & Soltani, 2017; Lau & Glimcher, 2007; Soltani & Wang, 2006, 2008; Sugrue et al., 2004).

Here, we used a novel experimental paradigm with a dynamic reward schedule to simultaneously measure the influences of reward value on choice between available targets and processing of visual information of these targets. We exploited the influence of visual motion on the trajectory of saccadic eye movements (Schafer & Moore, 2007) to quantify sensitivity to visual motion as a behavioral readout of visual processing in a criterion-free manner. Using this measure in the context of a saccadic free-choice task in monkeys allowed us to simultaneously estimate how reward feedback is integrated to determine both visual processing and decision making on a trial-by-trial basis. We fit choice behavior using multiple reinforcement learning models to examine how animals integrated reward outcomes over time and to estimate reward values on a trial-by-trial basis. In addition, we used correlation between integrated reward feedback on different timescales and our measure of sensitivity to visual motion in order to determine how sensitivity to visual motion is influenced by the estimated reward values.

Methods

Subjects. Two male monkeys (*Macaca mulatta*) weighing 6 kg (monkey 1), and 11 kg (monkey 2) were used as subjects in the experiment. The two monkeys completed 160 experimental sessions (74 and 86 sessions for monkeys 1 and 2, respectively) on separate days in the free-choice task for a total of 42,180 trials (10,096 and 32,084 trials for monkeys 1 and 2, respectively). Each session consisted of approximately 140 and 370 trials for monkeys 1 and 2, respectively. All surgical and behavioral procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care and the consultant veterinarian and were in accordance with National Institutes of Health and Society for Neuroscience guidelines.

Visual stimuli. Saccade targets were drifting sinusoidal gratings within stationary, 5°–8° Gaussian apertures. Gratings had a spatial frequency of 0.5 cycle/° and Michelson contrast between 2%–8%. Target parameters were held constant during an experimental session. Drift speed was 5°/s in a direction perpendicular to the saccade required to acquire the target. Targets were identical on each trial with the exception of drift direction, which was selected randomly and independently for each target.

Experimental paradigm. After acquiring fixation on a central fixation spot, the monkey waited for a variable delay (200–600 *ms*) before the fixation spot disappeared and two targets appeared on the screen simultaneously (**Fig. 1A**). Targets appeared equidistant from the fixation spot, and diametrically opposite one another. The monkeys had to make a saccadic eye movement to one of the two targets in order to select that target and obtain a possible reward allocated to it (see Reward schedule). Both targets disappeared at the start of the eye movement. If the saccadic eye movement shifted the monkey's gaze to within a 5–8°-diameter error window around the target within 400 *ms* of target appearance, the monkeys received a juice reward according to the variable reward schedule described below.

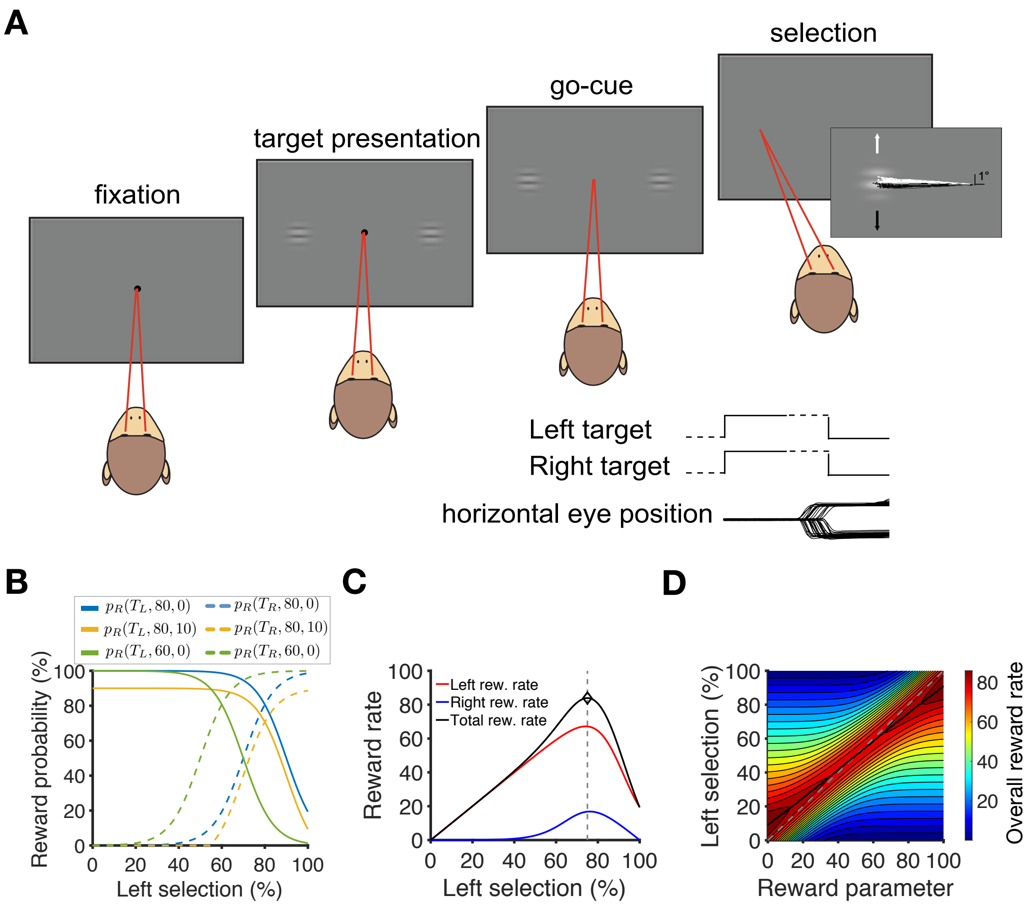

Figure 1. The free-choice task and reward schedule example. (**A**) Task design. On each trial, a fixation point appeared on the screen, followed by the presentation of two drifting-grating targets. The monkeys indicated their selection with a saccade. Targets were extinguished at the onset of the saccade. A juice reward was delivered on a variable schedule following the saccade. Event plots indicate the sequence of presentation of the visual targets; dashed lines denote variable time intervals. Horizontal eye position traces are from a subset of trials of an example experiment, and show selection saccades to both left target (T_L , downward deflecting traces) and right target (T_R , upward deflecting traces). (**B**) Examples of reward probability as a function of the percentage of left choices, separately for left and right targets ($p_R(T_L, r, x)$ and $p_R(T_R, r, x)$) for different values of reward parameter r and penalty parameter x (see Eq. 1). (**C**) Plotted is the reward harvest rate on each target as a function of the percentage of T_L selections, $f(T_L)$, for r=80 and x=0. (**D**) Total reward harvest rate as a function of r and the percentage of T_L selections. The gray dashed line shows $f(T_L) = r$ corresponding to matching behavior. The black solid line indicates the percentage of T_L selections that results in the optimal reward rate. Slight undermatching corresponds to optimal choice behavior in this task.

Quantifying the motion-induced bias. Eye position was monitored using the scleral search coil method (Fuchs & Robinson, 1966; Judge, Richmond, & Chu, 1980) and digitized at 500 Hz. Saccades were detected using previously described methods (Schafer & Moore, 2007). Directions of drifting gratings were perpendicular to the saccade required to choose the targets. Saccades directed to drifting-grating target are displaced in the direction of visual motion, an effect previously referred to as the motion-induced bias (MIB) (Schafer & Moore, 2007). The MIB for each trial was measured as the angular deviation of the saccade vector in the direction of the chosen target's drift, with respect to the mean saccade vector from all selections of that target within the session. In order to compare MIB values across sessions with different target contrasts and locations, MIB values were z-score normalized for each session to avoid confounds due to systematic biases.

Reward schedule. For each correct saccade, the monkey could receive a juice reward with a probability determined by a dynamic reward schedule based on the location of the foveated target (Abe & Takeuchi, 1993). More specifically, the probability of reward given a selection of the left (T_L) or right (T_R) target was equal to:

$$p_R(T_L, r, x) = \frac{1}{1 + \exp(-\frac{-f_L + r + 10}{s})} - x$$

$$p_R(T_R, r, x) = \frac{1}{1+\exp\left(-\frac{+f_L - r + 10}{s}\right)} - x \qquad \text{(Eq. 1)}$$

where f_L is the local fraction (in percentage) of T_L selections estimated using the previous 20 trials; *r* (reward parameter) is a task parameter that was fixed on a given session of the experiment and determined which option was globally more valuable (T_L for *r*>50, and T_R for *r*<50); *s* is another task parameter that determines the extent to which the deviation from matching (corresponding to f_L=*r*) results in a decrease in reward probability and was set to 7 in all experimental sessions; and x is a penalty parameter that reduced the global probability of a reward. Positive values of x decreased reward probability on saccades to both left and right targets in order to further motivate monkeys to identify and choose the more rewarding location at the time. x was kept constant throughout a session and was assigned to one of the following values on a fraction of sessions (reported in the parentheses in percentage): 0 (77%), 0.15 (6%), 0.30 (6%), or 0.40 (11%). Although the introduction of penalty decreased the reward probability and rate on both targets, it did not change the local choice fraction (f_L) at which the optimal reward rate or matching could be achieved.

Based on the above equations, the reward probabilities on saccades to left and right targets are equal at f_L=*r*, corresponding to matching behavior, which is slightly suboptimal in this task. As shown in **Fig. 1C, D**, an optimal reward rate is obtained via slight undermatching. As the value of *s* approaches zero, matching and optimal behavior become closer to each other.

Reinforcement learning models. In our experiment, reward was assigned based on target location (left vs. right) and thus the targets' motion directions were irrelevant for obtaining reward. Nevertheless, we considered the possibility that monkeys could incorrectly assign value to motion direction. We used various reinforcement learning (RL) models to fit choice behavior in order to determine whether monkeys attributed reward outcomes to target locations or target motions, and how they integrated these outcomes over trials to estimate reward values and guide choice behavior. Therefore, we considered RL models that learn reward value associated with target locations as well as RL models that learn reward values associated with the motion of the two targets.

In the models based on the location of the targets (location-based RLs), the left and right targets (T_L and T_R) were assigned reward values $V_L(t)$ and $V_R(t)$, respectively. In the models based on motion direction of the targets (motion-based RLs), reward values $V_U(t)$ and $V_D(t)$ were assigned to the upward and downward motion (T_U and T_D), respectively. For both types of models, values were updated at the end of each trial according to different learning rules described below. In addition, we assumed that the probability of selecting T_L (or T_U in motion-based RLs) is a sigmoid function of the difference in reward values as follows:

$$p\left(T_{L/U}\right) = \frac{1}{1+\exp(-(V_{L/U}(t)-V_{R/D}(t)-b))} \quad \text{(Eq. 2)}$$

where *b* quantifies the bias in choice behavior toward the left target (or upward motion), $V_{L/U}$ denotes the value of the left target in the location-based RL or upward motion in the motion-based RL, respectively. Similarly, $V_{R/D}$ denotes the value of the right target in the location-based RL or downward motion in the motion-based RL, respectively.

At the end of each trial, reward values of one or both targets were updated depending on the choice and reward outcome on that trial. We considered different types of learning rules for how reward outcomes are integrated over trials and grouped these learning rules depending on whether they estimate a quantity similar to *return* (average reward per selection) or *income* (average reward per trial). On the one hand, the monkeys could update reward value of the chosen target only, making the estimated reward values resemble local (in time) return. On the other hand, reward values of both the chosen and unchosen targets could be updated, making these values resemble local income. This grouping was done because previous work has shown that both local return and income can be used to achieve matching behavior (Soltani & Wang, 2006). In addition, reward values for the chosen and unchosen targets could decay similarly or differently, and monkeys could learn differently from positive (reward) and negative (no reward) outcomes. We tested these possibilities using four different types of RL models.

In return-based RL models (RL$_{\text{ret}}$), only the value of the chosen target (in terms of location or motion direction) was updated. More specifically, if T_L (T_U) was selected and rewarded on trial *t*, reward values were updated as the following:

$$\begin{aligned} V_{L/U}(t+1) &= \alpha V_{L/U}(t) + \Delta_r \\ V_{R/D}(t+1) &= V_{R/D}(t) \end{aligned} \qquad \text{(Eq. 3)}$$

where Δ_r quantifies the change in reward value after a rewarded trial and α is the decay rate. If T_L (T_U) was selected but not rewarded, reward values of the two target locations or motion directions were updated as the following:

$$\begin{aligned} V_{L/U}(t+1) &= \alpha V_{L/U}(t) + \Delta_n \\ V_{R/D}(t+1) &= V_{R/D}(t) \end{aligned} \qquad \text{(Eq. 4)}$$

where Δ_n quantifies the change in reward value after a non-rewarded trial. Similar equations governed the update of reward values when T_R (T_D) was selected. Importantly, in these models, reward value of the unchosen target (in terms of location or motion) is not updated, making these models return-based.

In contrast, in all other models, reward values of both chosen and unchosen targets were updated in every trial, making them income-based models. Specifically, in the RL$_{\text{Inc}}$(1) models, the value of the unchosen target decayed at a rate similar to the value of the chosen target. For example, when T_L (T_U) was selected, the values were updated as follows:

$$\begin{aligned} V_{L/U}(t+1) &= \alpha V_{L/U}(t) + \Delta_r \text{ (or } \Delta_n \text{ for no-reward)} \\ V_{R/D}(t+1) &= \alpha V_{R/D}(t). \end{aligned} \qquad \text{(Eq. 5)}$$

In the RL$_{\text{Inc}}$(2) models, the value of chosen and unchosen targets decayed differently:

$$\begin{aligned} V_{L/U}(t+1) &= \alpha_c V_{L/U}(t) + \Delta_r \text{ (or } \Delta_n \text{ for no-reward)} \\ V_{R/D}(t+1) &= \alpha_u V_{R/D}(t) \end{aligned} \qquad \text{(Eq. 6)}$$

where α_c, and α_u are the decay rates for the chosen and unchosen targets or motion directions.

In the RL$_{\text{Inc}}$(3) models, we updated the value of unchosen target location (or unchosen motion direction) in addition to decaying the values of chosen and unchosen locations:

$$\begin{aligned} V_{L/U}(t+1) &= \alpha_c V_{L/U}(t) + \Delta_r \text{ (or } \Delta_n \text{ for no-reward)} \\ V_{R/D}(t+1) &= \alpha_u V_{R/D}(t) + \Delta_u. \end{aligned} \qquad \text{(Eq. 7)}$$

Note that the motion directions of the two targets were the same in half of the trials. This makes updating of motion values non-trivial in trials in which the chosen and unchosen motion directions are the same (referred to as match trials). Therefore, we tested different update rules for match trials to identify the model that best describes the monkeys' choice behavior. Specifically, we tested two possibilities: 1) update the motion direction that was presented on a given match trial only; 2) update both present and non-present motion directions but in the opposite direction. We found that the second model, in which the value of both motion directions were updated, provided a better fit for our data (data not shown).

Finally, we also tested hybrid RL models in which the values of both target locations and motion directions were updated at the end of each trial, and subsequently used to make decisions. Fitting based on these hybrid models were not significantly better than those using the RL models that consider only the values of target locations. Therefore, the results from these hybrid models are not presented here.

Model fitting and comparison. We used the maximum likelihood ratio method to fit choice behavior with different RL models described above and estimated the parameters of those models. To compare the goodness-of-fit based on different models while considering the number of model parameters, we used the negative log-likelihood (-*LL*), Akaike information criterion (AIC) and Bayesian information criterion (BIC). AIC is defined as:

$$AIC = -2 \times LL + 2 \times k \qquad \text{(Eq. 8)}$$

where LL is log-likelihood of the fit and k is the number of parameters in a given model. BIC is defined as:

$$BIC = -2 \times LL + \ln{(n)} \times k \qquad \text{(Eq. 9)}$$

where LL is log-likelihood of the fit, k is the number of parameters in a given model, and n is the number of trials in a given session.

Effect of reward value on the MIB. In order to estimate reward values associated with the two target locations, we used two methods corresponding to income and return values. To calculate the income value of a given target location, we filtered the sequences of reward outcomes on preceding trials using an exponential filter with a given time constant τ, assigning +1 to rewarded trials and Δ_n to non-rewarded trials if that target location was chosen and 0 if that target location was not chosen on the trial. To calculate the return value of a given target location, we filtered reward sequence on trials in which that target location was chosen using an exponential filter with a given time constant τ, assigning +1 to rewarded trials and Δ_n to non-rewarded trials. Finally, we calculated the correlation between the MIB and the obtained filtered values for different values of τ and Δ_n.

Data analysis. To assess the overall performance of the monkeys, we used static and dynamic models to harvest maximum rewards. In the static model, we assumed that selection between the two target locations in a given session was a stochastic process with a fixed probability. We therefore replaced f_L in Eq.1 with the probability of T_L selection, $p(T_L)$. Therefore, the reward rate on T_L and T_R were equal to $p(T_L) \times p_R(T_L, r, x)$ and $(1 - p(T_L)) \times p_R(T_R, r, x)$), respectively. The optimal choice probability was then computed by finding $p(T_L)$ for which the sum reward rate from the two targets was maximal. In the dynamic model, the target location with the larger probability of reward or return ($p_R(T_L, r, x)$ or $p_R(T_R, r, x)$) is selected on each trial.

We also compared the monkeys' choice behavior with the prediction of the matching law. The matching law states that the animals allocate their choices in a proportion that matches the relative reinforcement obtained by the choice options. In our experiment, this is equivalent to the relative fraction of left (respectively, right) choices to match the relative fraction of incomes on the left (respectively, right) choices. Therefore, to quantify deviations from matching, we calculated the difference between the relative fraction of choosing the more rewarding target (left when r >50 and right when r <50) and the relative fraction of the income for the more rewarding target. Negative and positive values correspond to undermatching (choosing the better option less frequently than the relative reinforcement) and overmatching, respectively.

Results

We trained two monkeys to freely select between two visual targets via saccadic eye movement (**Fig. 1A**). Saccades to each target resulted in delivery of a fixed amount of juice reward with a varying probability. Targets were stationary apertures of drifting gratings and the reward probability was determined based on the location of the grating targets independently of the direction of visual motion contained within the gratings. More specifically, on a given trial, probabilities of reward on the left and right targets were determined by the reward parameter (r) and the choice history on the preceding 20 trials (Eq. 1; **Fig. 1B**). Critical for our experimental design, the motion contained within the targets caused the endpoints of eye movements made to those targets to be systematically biased in the direction of grating motion. We first show that this motion-induced bias can be used as a measure of sensitivity to visual motion on a trial-by-trial basis.

MIB measures sensitivity to visual motion. The motion-induced bias (MIB) of a saccadic eye movement quantifies the extent to which the endpoints of saccades directed toward the drifting gratings were biased in the direction of grating motion (**Fig. 1A**, **Fig. 2A**). Despite the stationary position of the grating aperture, motion in the drifting sinusoid nonetheless induces a shift in the perceived position of the aperture in human subjects (De Valois & De Valois, 1991) and biases saccadic endpoints in the direction of grating drift (MIB) in monkeys (Schafer & Moore, 2007). By examining the MIB in different conditions, we established that it can provide a measure of sensitivity to visual motion even when the grating motion is not behaviorally relevant.

First, we found that the magnitude of the MIB depended on the grating contrast. More specifically, the MIB increased by 27% when the (Michaelson) contrast of grating increased from 2% to 3% (two-sided independent measures t-test, p=$7.85 * 10^{-9}$; **Fig. 2B**). Second, we observed that the MIB depended almost exclusively on the motion direction of the selected target as it was only slightly affected by non-matching motion in the unchosen target (**Fig. 2C**). Specifically, the average z-score normalized MIB measured in two monkeys across all trials (mean = 0.38) was altered by only 9% when the unchosen target differed in direction of the grating motion. Together, these results demonstrate that the MIB in our task is sensitive to the properties of sensory signal (grating motion direction and contrast) and thus, can be used to measure the influence of internal factors such as subjective value on visual processing.

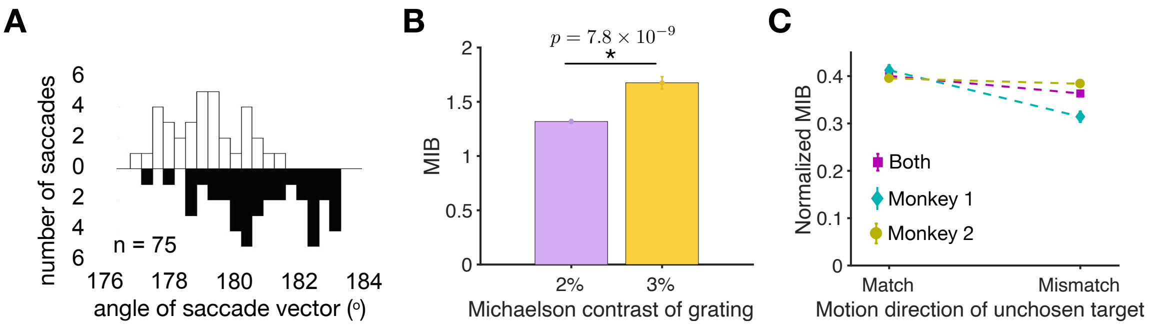

Figure 2. MIB measures sensitivity to visual motion. (**A**) Plotted are the example distributions of the angle of saccade vector (relative to the fixation dot) for upward (open) and downward (filled) drifting targets. (**B**) MIB significantly increased as the contrast of grating is increased from 2% (purple) to 3% (yellow). (**C**) Comparison of the normalized MIB when the directions of motion in the chosen and nonchosen targets matched or did not match. The MIB is normalized for each monkey separately within each sessions.

Global effects of reward on choice behavior. To examine the overall effects of reward schedule on the monkeys' choice behavior, we first measured how the monkeys' choice behavior tracked the target location that was globally more valuable. We found that target selection was sensitive to the reward parameter in both monkeys and the harvested reward rate was high, averaging 0.66 and 0.65 across all sessions (including those with penalty) in monkeys 1 and 2, respectively (**Fig. 3A, B, D, E**). To better quantify the monkeys' performance, we also computed the overall harvested reward by a model that selects between the two targets with the optimal but fixed choice probability in a given session (optimal static model; see example in **Fig. 1C**) or a model in which the target with higher probability of reward was chosen on each trial (optimal dynamic model). We found that performance of both monkeys was sub-optimal; however, the pattern of performance as a function of reward parameter for monkeys 1 and 2 resembled the behavior of the optimal static and dynamic models, respectively (**Fig. 3B, E**). Since each session of the experiment for monkey 2 was longer, we confirmed that there was no significant difference in task performance between the first and second halves of sessions for monkey 2 (difference mean±sem: 0.003 ± 0.008; two-sided paired t-test, $p = 0.7, d = 0.03$). Together, these results suggest that both monkeys followed the reward schedule on each session closely whereas their choice behavior was suboptimal.

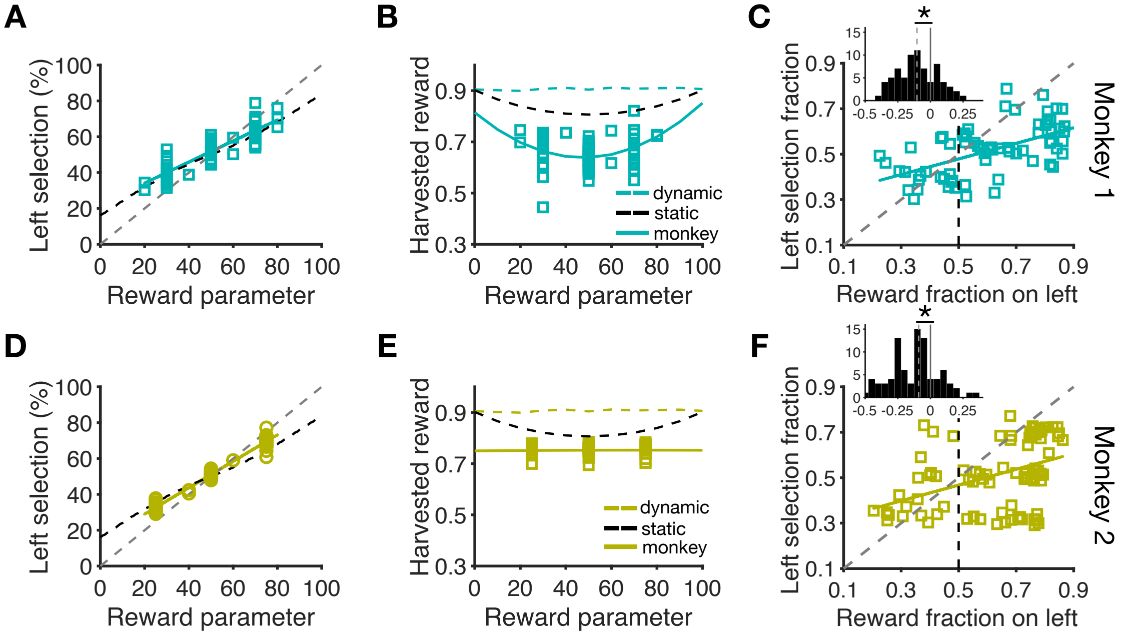

Figure 3. Global effects of reward on choice behavior. (**A**) Choice behavior is sensitive to reward parameter. Percentage of T_L selections is plotted as a function of r, which varied across experimental sessions for monkey 1. The colored lines are linear fits, and the black dashed line shows the optimal $f(T_L)$ for a given value of r assuming selection between the two targets with a fixed probability (optimal static model). The gray dashed line shows unit slope. (**B**) The overall performance was suboptimal. Plotted is harvested rewards per trial as a function of reward parameter r for zero penalty sessions for monkey 1. The solid colored lines show fit using a quadratic function. The colored and black dashed lines indicate harvested reward rates of the optimal dynamic and static models, respectively. (**C**) Proportion of T_L selections is plotted as a function of the fraction of harvested reward on the left target. The colored lines are linear fits and the gray dashed line shows the diagonal line corresponding to matching behavior. Monkey 1 showed significant under-matching by selecting the more rewarding target with a choice fraction smaller than reward fraction. The inset shows the difference between choice and reward fractions with negative and positive values corresponding to under- and over-matching. The gray dashed lines indicate the medians of the distributions and asterisks show the significant difference from 0 (i.e. matching) using Wilcoxon signed rank test (p<.05). (**D–F**) Similar to panels A-C but for monkey 2.

We also examined the global effects of reward on choice by measuring matching behavior. To that end, we compared choice and reward fractions on each session and found that both monkeys exhibited undermatching behavior (**Fig. 3C, F**). More specifically, they selected the more rewarding location with a probability that was smaller than the relative reinforcement obtained on that location (monkey 1 median(choice fraction – reward fraction) $= -0.103$; Wilcoxon signed rank test, $p = 2.43 \times 10^{-6}, d = 0.65$; **Fig. 3C** inset; monkey 2 median(choice fraction – reward fraction) $= -0.09$, $p = 1.41 \times 10^{-7}, d = 0.67$; **Fig. 3F** inset). Furthermore, the degree of undermatching was similar for the two monkeys (diff $= 0.013$; Wilcoxon rank sum test, $p = 0.58, d = 0.05$).

Global effects of reward on sensitivity to visual motion. To examine the global effects of reward on sensitivity to visual motion, we tested whether the average MIB on the two target locations was influenced by the reward schedule. More specifically, we computed the correlation between the difference in the session-based average MIB for saccades to the more and less rewarding target locations and reward parameter in each session but did not find any evidence for such correlation for either of the two monkeys (Spearman correlation; monkey 1: $r = 0.04$, $p = 0.8$; monkey 2: $r = 0.11$, $p = 0.39$). We also examined whether the average MIB for all saccades in a given session was affected by the overall performance in that session. However, we did not find any evidence for correlation between the session-based average MIB and performance for either of the two monkeys (Spearman correlation; monkey 1: $r = -0.07, p = 0.54$; monkey 2: $r = 0.13, p = 0.21$). These results suggest that unlike choice behavior, sensitivity to visual motion is not affected by the global reward value of the target location or the overall reward rate in a given session (i.e., overall motivation).

Effects of local reward value on choice behavior. The analyses presented above show how the overall choice behavior was influenced by the global reward value of the two target locations in a given session (determined by the reward parameter *r*). However, reward probability on a given trial was not only determined by *r* but also by the monkeys' choices on the preceding trials. More importantly, immediate reward outcomes could strongly influence choice independently of the location that was more rewarding globally.

To investigate how reward outcomes were integrated to guide the monkeys' choice behavior on each trial, we used multiple reinforcement learning (RL) models to fit the choice behavior of individual monkeys on each session of the experiment. These models assume that selection between the two targets is influenced by reward values associated with each target, which are updated on each trial based on reward outcome (see Methods). Although reward was assigned based on the location of the two targets (left vs. right) in our experiment, the monkeys could still assume that motion direction is informative about reward. Therefore, we considered RL models that learn reward value associated with target locations as well as RL models that learn reward values associated with the motion of the two targets using four different learning rules. Considering the observed undermatching behavior, we grouped learning rules depending on whether they result in the estimation of reward value in terms of local (in time) return or income.

In $\mathrm{RL}_{\mathrm{ret}}$ models, only the value of the chosen target (in terms of location or motion) was updated, making them return-based models. In $\mathrm{RL}_{\mathrm{Inc}}(1)$ models, in addition to updating the value of the chosen target, the value of the unchosen target decayed at a rate similar to the value of the chosen target, making these models income-based. In $\mathrm{RL}_{\mathrm{Inc}}(2)$ models, the value of chosen and unchosen targets were allowed to decay at different rates. Finally, in $\mathrm{RL}_{\mathrm{Inc}}(3)$ models, we also assumed a change in the value of the unchosen target or motion direction in addition to the decay. Because the value of both chosen and unchosen target locations were updated on each trial in $\mathrm{RL}_{\mathrm{Inc}}(2)$ and $\mathrm{RL}_{\mathrm{Inc}}(3)$ models, we refer to these models as income-based similarly to $\mathrm{RL}_{\mathrm{Inc}}(1)$. However, we note that only $\mathrm{RL}_{\mathrm{Inc}}(1)$ models are able to estimate local income accurately.

We first compared the goodness-of-fit between the location-based and motion-based RLs using negative log likelihood (*-LL*), Akaike information criterion (AIC), and Bayesian information criterion (BIC) in order to test which of the two types of models can predict choice behavior better. Such comparisons based on the three measures yield the same results because the two types of models have the same number of parameters for a given learning rule. We found that for both monkeys, all the location-based models outperformed the motion-based RLs (**Table 1**). This demonstrates that both monkeys attributed reward outcomes to target locations more strongly than to target motions, and used value attributed to target locations to perform the task.

After establishing that monkeys used target location to integrate reward outcomes, we next examined how this integration was performed by comparing the quality of fit in location-based models with different learning rules. We found that for monkey 1, $\mathrm{RL}_{\mathrm{ret}}$ and $\mathrm{RL}_{\mathrm{Inc}}(1)$ models provided the best fit of choice data; although goodness-of-fit measures were not significantly different between these models, these models provided better fits than the RL$_{\text{Inc}}$(2) and RL$_{\text{Inc}}$(3) models (**Fig. 4**). Interestingly, fitting choice behavior with the RL$_{\text{Inc}}$(1) model resulted in learning rates (α) that were close to 1 for many sessions (mean and median of α were equal to 0.77 and 1.0, respectively). This result indicates that monkey 1 integrated reward over many trials to guide its choice behavior. This is compatible with the pattern of performance as a function of reward parameter for this monkey (**Fig. 3B**), which resembles the pattern of the optimal static model.

	RL$_{\text{ret}}$	**RL$_{\text{Inc}}$(1)**	**RL$_{\text{Inc}}$(2)**	**RL$_{\text{Inc}}$(3)**
Monkey 1	Δ(-LL, AIC, or BIC)=−5.48 p=2.55 ∗ 10^{-7}	Δ(-LL, AIC, or BIC)=−7.19 p=2.58 ∗ 10^{-9}	Δ(-LL, AIC, or BIC)=−6.53 p=1.39 ∗ 10^{-8}	Δ(-LL, AIC, or BIC)=−8.06 p=5.32 ∗ 10^{-10}
Monkey 2	Δ(-LL, AIC or BIC)=−60.96 p=2.74 ∗ 10^{-21}	Δ(-LL, AIC or BIC)=−105.71 p=2.58 ∗ 10^{-26}	Δ(-LL, AIC, or BIC)=−103.46 p=2.58 ∗ 10^{-26}	Δ(-LL, AIC, or BIC)=−107.25 p=2.58 ∗ 10^{-26}

Table 1. Comparison of goodness-of-fit between location-based and motion-based RL models using -LL, AIC or BIC. Δ(-LL, AIC, or BIC) shows the median of the difference between location-based and motion-based RL models fitted for each session separately. Note that all differences in goodness-of-fit measures (based on -LL, AIC, and BIC) are similar because the number of parameters is the same across location-based and motion-based models. *P*-values indicate the significance of the statistical test (two-sided sign-test) for comparing the goodness-of-fit between the location-based and motion-based RLs.

The same analysis for monkey 2 revealed a similar integration of reward outcomes but on a different timescale. More specifically, we found that the RL$_{\text{Inc}}$(1) model provided the best fit for choice behavior as the goodness-of-fit in this model was better than the return-based model (RL$_{\text{ret}}$) and more detailed income-based (RL$_{\text{Inc}}$(2), and the RL$_{\text{Inc}}$(3)) models (**Fig. 4**). In contrast to monkey 1, the estimated learning rate based on the RL$_{\text{Inc}}$(1) model were much smaller than 1 for many sessions for monkey 2 (mean and median α were equal to 0.32 and 0.33, respectively). These results indicate that monkey 2 integrated reward over a shorter timescale (a few trials) to guide its choice behavior. This is compatible with the pattern of performance as a function of reward parameter for this monkey (**Fig. 3E**), which resembles the pattern of the optimal dynamic model.

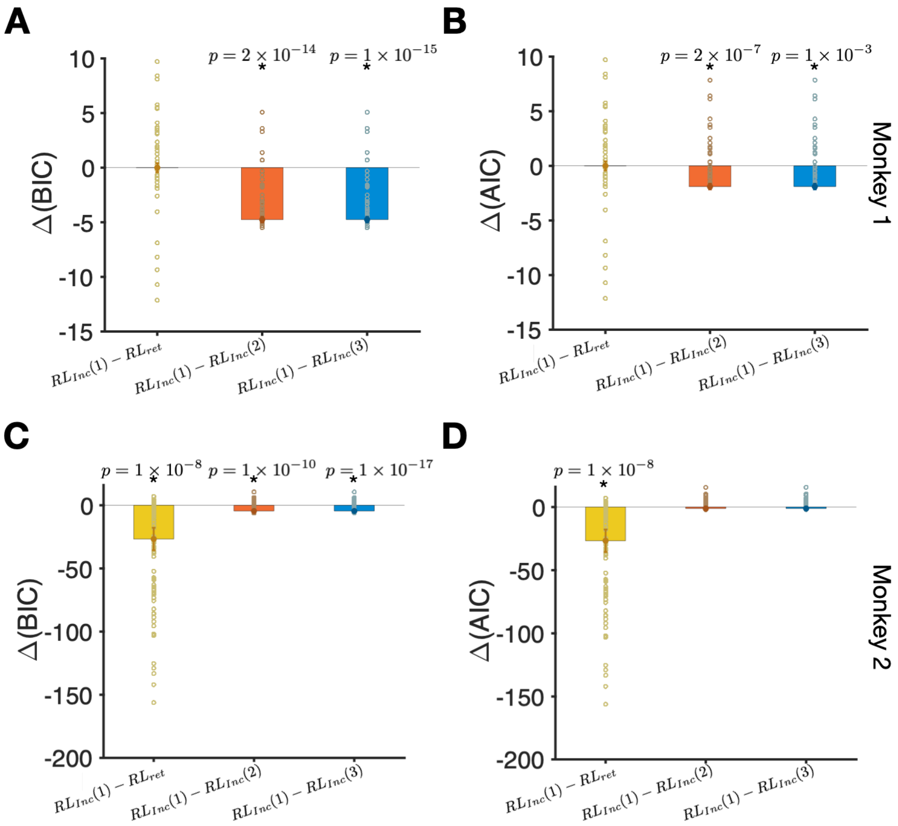

Figure 4. Comparison of goodness-of-fit between different location-based RL models reveals that $\mathrm{RL_{Inc}}(1)$ model provided the best overall fit. (**A**) Each point shows the difference between BIC for fits based on the $\mathrm{RL_{Inc}}(1)$ model and the three competing models (indicated on the x-axis) in a session of the experiment. Bars show the median of the difference in BIC and errors are s.e.m. Reported *p*-value are based on a two-sided sign test. For monkey 1, fits based on the $\mathrm{RL_{Inc}}(1)$ and $\mathrm{RL_{ret}}$ models were not significantly different. (**B**) The same as in A but based on the difference in AIC . (**C–D**) Similar to panels A and B but for monkey 2.

Together, fitting of choice behavior shows that both monkeys associated reward outcomes with the location of the chosen target. Moreover, both monkeys estimated reward values in terms of income by integrating reward outcomes over multiple trials and used these estimated reward values to make decisions.

Effects of local reward value on sensitivity to visual motion. In addition to choice, our experimental design also allows us to measure the MIB and thus the sensitivity to visual motion on each trial of the experiment. Importantly, as neither the direction of target motion nor the magnitude of the MIB had any impact on reward probability or obtaining reward (i.e., processing of motion direction was not required to obtain a reward), the MIB provided an implicit trial-by-trial measure of sensitivity to visual motion that was independent of target choice. Because we expected that reward values of the targets would affect both visual processing and choice between the targets, we examined whether the MIB was influenced by reward obtained on preceding trials, and if so, how reward feedback was integrated to influence the MIB.

First, we studied whether reward feedback had an immediate effect on the MIB in the following trial. We found that the MIB was larger in the trials that were preceded by a rewarded rather than unrewarded trials (mean±s.e.m.: 0.03±0.009; two-sided t-test, $p = 6.95 \times 10^{-4}, d = 0.18$). When considered data from each monkey individually, this effect only retained significance for monkey 1 (monkey 1: mean±s.e.m.: 0.05±0.01; two-sided t-test, $p = 6.5 \times 10^{-4}, d = 0.09$; monkey 2: mean±s.e.m.: 0.01±0.01; two-sided t-test, $p = 0.21, d = 0.09$). These results suggest that the MIB is affected by the immediate reward outcome in the preceding trial.

In the previous section, we showed that the best model for fitting choice behavior was one that estimates reward value based on the income on each target location and uses the difference in incomes to drive choice behavior ($\text{RL}_{\text{Inc}}(1)$ model) (**Fig. 4**). However, it is not clear if the MIB is influenced by reward values of the two targets in a similar fashion. To test this relationship, we computed correlations between the trial-by-trial MIB and reward values of the chosen target location, the unchosen target location, and their sum and difference. We considered reward values based on both income and return (see Methods).

We made several key observations. First, we found that the MIB was positively correlated with reward value of both the chosen and the unchosen target (**Fig. 5A-B, Fig. 5E-F**) and as a result, was most strongly correlated with the sum of reward values of the two targets (**Fig. 5C, Fig. 5G**). In contrast to choice, the MIB was poorly correlated with the difference in reward values of the chosen and unchosen target (**Fig. 5D**, **Fig.5H**, **Supplementary Fig. 1**). Therefore, choice was most strongly correlated with the difference in reward values, whereas the MIB was most strongly correlated with the sum of reward values from the two targets. Second, although the aforementioned relationships were true for reward value based on return and income, we found that correlations between the MIB and return values were stronger than correlations between the MIB and income values (compare **Fig. 5** and **Supplementary Fig. 2**). Third, the maximum correlation occurred for the values of τ at around 15–20 trials and for negative values of Δ_n, similarly for both monkeys. This result indicates that for both monkeys, the MIB was influenced by reward integrated over many trials, and the absence of reward on a given trial had a negative influence on the MIB on the following trial ($\Delta_n < 0$).

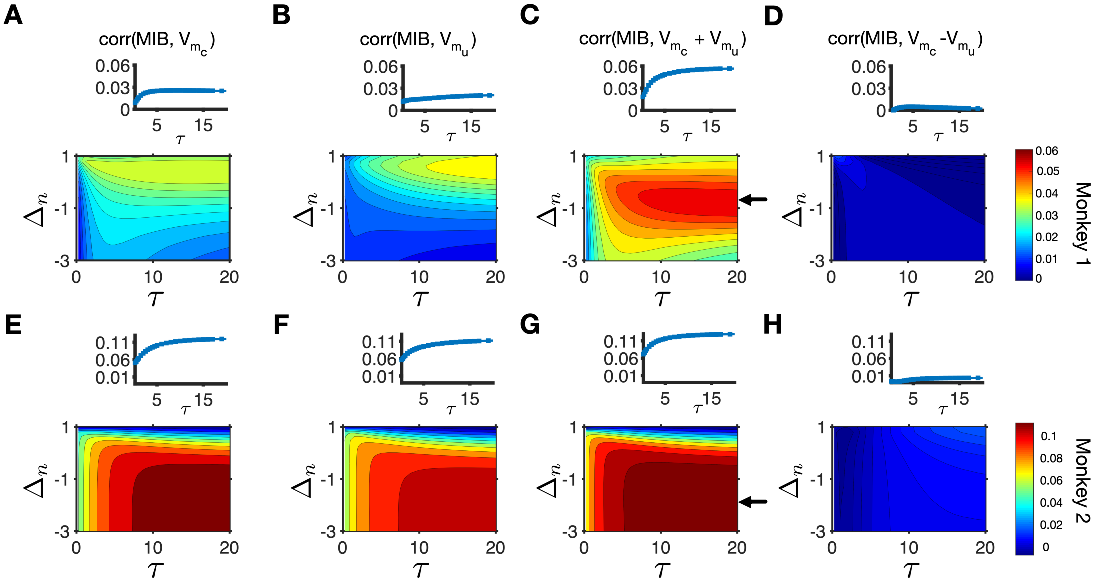

Figure 5. MIB was correlated with the sum of estimated return values of the two targets. (**A–D**) Plotted are the correlations between the MIB and estimated return values of the chosen (A) and unchosen (B) targets, and their sum (C) and their difference (D) for different values of τ and Δ_n. The inset in each panel shows the correlation between the MIB and the corresponding estimated return values for different values of τ and a specific value of Δ_n (indicated with an arrow in the main panel C) for monkey 1. (**E–H**) The same as in A-D but for monkey 2.

Finally, to better illustrate distinct effects of reward on decision making and visual processing, we used two sets of parameters (τ = 15 and $\Delta_n = 0$, τ = 15 and $\Delta_n = -0.5$) that resulted in significant correlations between choice and reward values and between the MIB and reward values in all cases, in order to generate separate series of reward values for each monkey. We then grouped trials into bins according to reward values of T_L and T_R for choice, or of the chosen and unchosen targets for the MIB, and computed the average probability of choosing the left target and the average MIB for each bin. We found that the probability of choosing the left target for both monkeys was largely determined by the difference in reward values of the left and right targets, as can be seen from contours being parallel to the diagonals (**Fig. 6A, B, E, F**). In contrast, the MIB was largely determined by the sum of reward values, as can be seen from contours being parallel to the second diagonals (**Fig. 6C, D, G, H**). These results clearly demonstrate that reward value has distinct effects on choice behavior and sensitivity to motion.

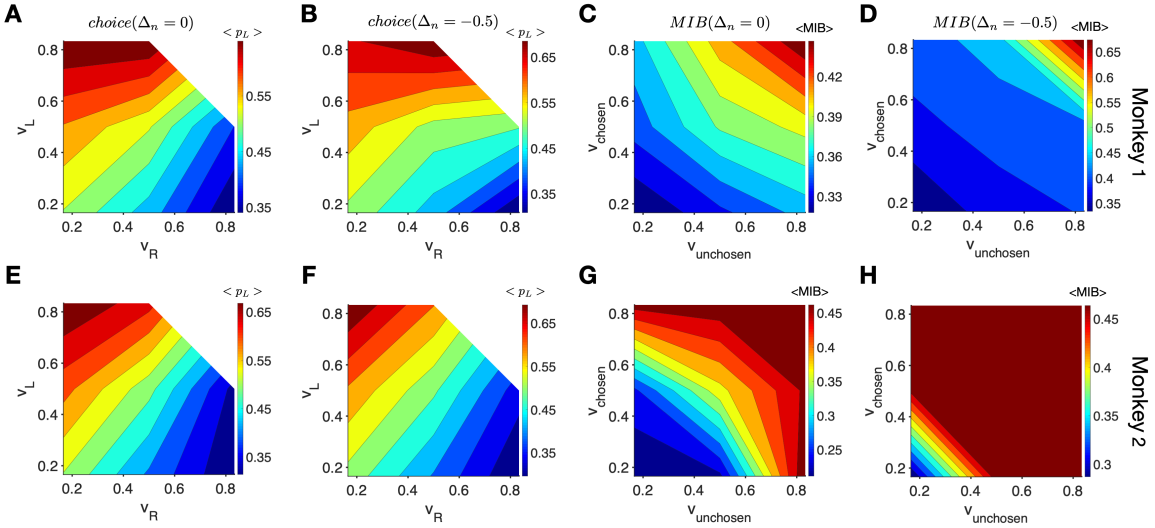

Figure 6. The choice probability for both monkeys was largely determined by the difference in reward values whereas the MIB was largely determined by the sum of reward values of targets. (**A–B**) Plots show the probability of choosing the left target as a function of reward values of the left and right targets for monkey 1, using τ = 15 and two values of Δ_n as indicated on the top. (**C–D**) Plots show the MIB as a function of reward values of the chosen and unchosen targets for monkey 1, using τ = 15 and two values of Δ_n as indicated on the top. (**E–H**) The same as in A-D but for monkey 2.

Discussion

Experimental paradigms with dynamic reward schedules have been extensively used in different animal models to study how reward shapes choice behavior on a trial-by-trial basis (Barraclough et al., 2004; Donahue & Lee, 2015; Herrnstein, Loewenstein, Prelec, & Vaughan, 1993; Lau & Glimcher, 2005; Li, McClure, King-Casas, & Montague, 2006; Sugrue et al., 2004). A general finding is that animals integrate reward outcomes on one or more timescales in order to estimate reward value and determine choice. In contrast, the influence of reward on selective processing of visual information, which is often described as attentional deployment, has been mainly studied using fixed reward schedules with unequal reward outcomes (B. A. Anderson et al., 2011a, 2011b; Barbaro et al., 2017; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010, 2014; Hickey & Peelen, 2017; Peck et al., 2009). The main findings from these studies are that targets or features associated with larger reward can more strongly capture attention and alter visual processing immediately or even after extended periods of time (reviwed in B. A. Anderson, 2013, 2016).

However, it has proven difficult to link the effects of reward value on saccadic choice and selective processing of visual information mainly because of separate measurements of these effects in different tasks. Indeed, the poorly described relationship between reward expectation and the processing of visual information has been implicated as a confounding factor in the interpretation of many past behavioral and neurophysiological results (Maunsell, 2004, 2015). An exception to this is a study by Serences (2008) in which the author utilized a task with dynamic reward schedule to demonstrate that the activity in visual cortex is modulated by reward history (i.e., integrated reward outcomes over many trials). Compatible with these results, we find that processing of visual information is affected by reward value estimated by integration of reward outcomes over many trials.

Using tasks designed specifically to dissociate value from a target's behavioral significance, or salience, a few studies have identified brain areas that respond primarily to the expected reward or the salience of a target (or both) in various species including rats (Lin & Nicolelis, 2008), monkeys (Roesch & Olson, 2004), and humans (Anderson et al., 2003; Cooper & Knutson, 2008; Jensen et al., 2007; Litt, Plassmann, Shiv, & Rangel, 2011). However, in these studies, the saliency signal observed in neural responses might reflect a number of different processes, such as motivation, attention, motor preparation, or some combination of these. In the present work, we exploited the influence of visual motion on saccades as an independent and implicit measure of visual processing during value-based decision making. This enabled us for the first time to measure choice and visual processing simultaneously and to test whether reward value has differential effects on these two processes.

Although motion was not predictive of reward and thus processing of motion direction was not required to obtain a reward, we found that similar to decision making, visual processing was influenced by reward values of the two targets. However, reward values of the two targets affected visual processing differently than how they affected choice in three ways. First, although choice was correlated most strongly with the difference between reward values of chosen and unchosen targets, visual processing was most strongly correlated with the sum of reward values of the two targets. The latter indicates that the overall reward value of targets in a given environment could influence the quality of sensory processing in that environment. Second, choice was more strongly affected by the income value of the target whereas MIB was more strongly affected by return values of the targets. Third, the time constant of reward integration, and the impact of no-reward were different between decision making and processing of target motion. These results point to multiple systems for reward integration in the brain.

We found certain differences between the results for the two monkeys that could indicate that they used different, idiosyncratic strategies for performing the task. For example, fitting results of reinforcement learning models indicated that monkey 1 used the reward history over many trials to direct its choice behavior. In contrast, monkey 2 used the reward history over few trials to direct its choice behavior. This difference was also apparent in the correlation between choice and the difference in reward values. Despite this difference in integration time constant, choice in both monkeys was most strongly correlated with the difference between reward values of the two targets. Furthermore, the MIB for both monkeys was most strongly correlated with the sum of reward values of the two targets, even though they integrated reward outcomes on different timescales.

The observed differences in reward effects on visual processing and decision making have important implications for the involved brain structures and underlying neural mechanisms. First, they suggest that brain structures involved in decision making and processing of visual information receive distinct sets of value-based input; e.g., ones that integrate reward over a different number of trials. The set of input affecting decision making carries information about reward value of individual targets whereas the set that affects visual processing carries information about the sum of reward values. Indeed, there are more neurons in the anterior cingulate cortex and other prefrontal areas that encode the sum value of available options than reward value of a given option (Kim, Hwang, Seo, & Lee, 2009), and these neurons might contribute to enhanced sensory processing. The frontal eye field (FEF) also receives inputs from the supplementary eye field (SEF), which contains neurons whose activity reflects reward value of the upcoming saccade (Chen & Stuphorn, 2015). Such input from the SEF could drive target selection in the FEF. Importantly, our findings can be used in future experiments to tease apart neural substrates by which reward value influences visual processing and decision making.

Second, a plausible mechanism that could contribute to the observed differences in the effects of reward is the differential influence of dopaminergic signaling on the functions of FEF neurons. Recent work demonstrates that the modulatory influence of the FEF on sensory activity within visual cortex is mediated principally by D1 receptors, and that D2-mediated activity is not involved (Noudoost & Moore, 2011). However, activity mediated through both receptor subtypes contributes to target selection, albeit in different ways (Noudoost & Moore, 2011; Soltani, Noudoost, & Moore, 2013). This evidence indicates that the neural mechanisms underlying target selection and visual processing are separable if only in terms of the involvement of different dopaminergic signals. Considering the known role of dopamine in reward processing (Schultz, 2007) and synaptic plasticity (Calabresi, Picconi, Tozzi, & Di Filippo, 2007), these two dopaminergic signaling pathways may provide a mechanism for the separate effects of reward on sensory processing and selection.

Third, in most choice tasks with dynamic reward schedules, local return and income are typically correlated, and the question of which quantity is the critical determinant of behavior has been debated for many years (Corrado, Sugrue, Seung, & Newsome, 2005; Gallistel & Gibbon, 2000; Gallistel, Mark, King, & Latham, 2001; Herrnstein & Prelec, 1991; Mark & Gallistel, 1994; Soltani & Wang, 2006; Sugrue et al., 2004). The observation that differences in local income are a better predictor of choice behavior may reflect the fact that local income provides information about which target is globally more valuable in each session of the task. In contrast, the dependence of visual processing on the sum of local return is more unexpected. The fact that visual processing is more strongly correlated with the return, which only changes with subsequent selections of the same target, indicates that this visual processing may more strongly depend on target-specific reward integration.

Finally, the separable influences of reward could be crucial for flexible behavior. For example, processing of visual information of the saccade target based on the sum of reward values could allow processing of information from the less rewarding target and thus, improve exploration. Future studies are needed to test whether disruption of this processing can reduce flexibility in target selection and choice behavior.

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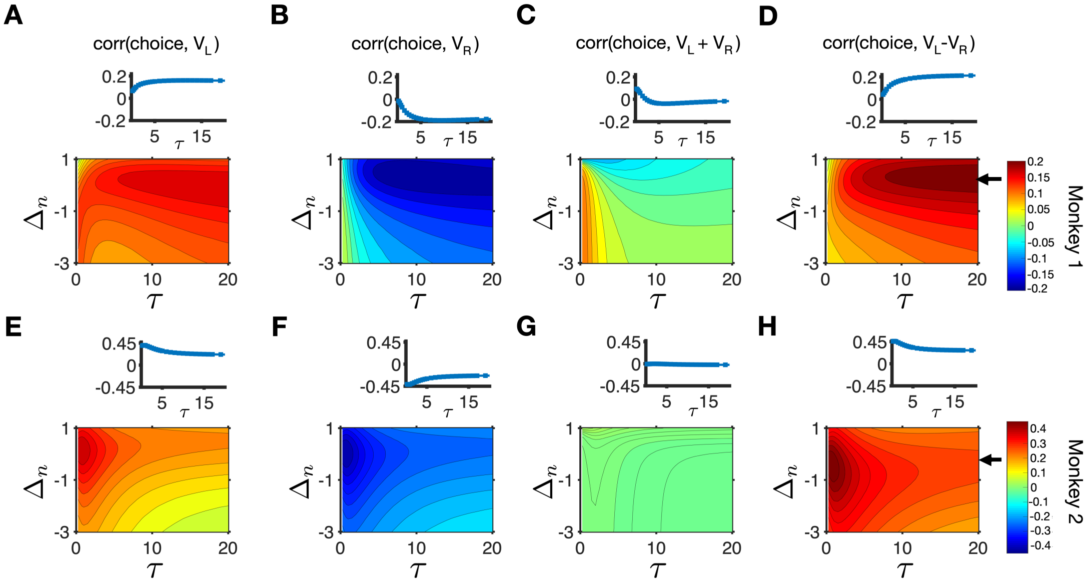
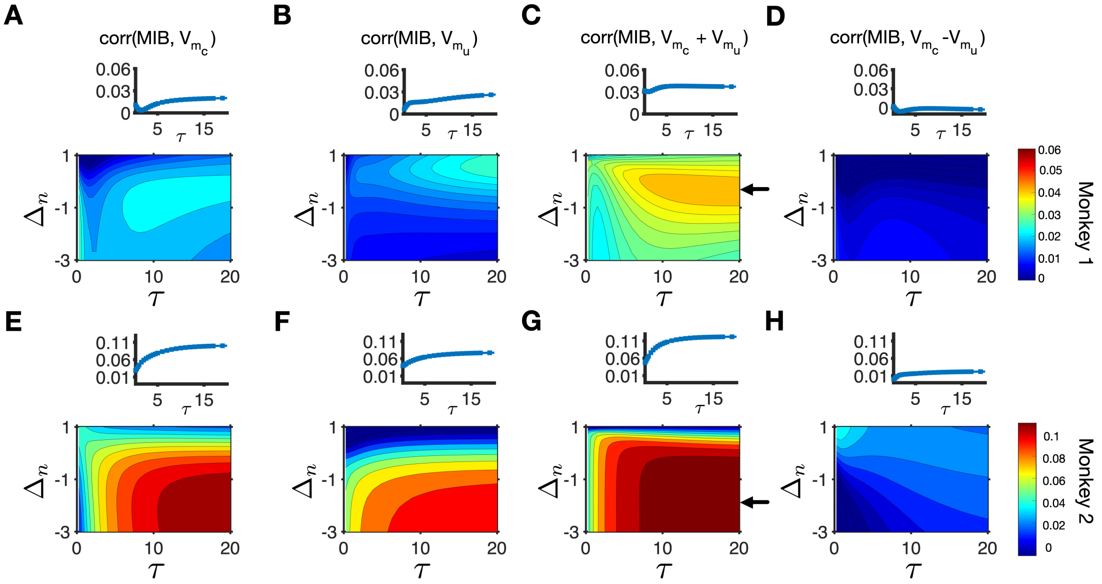
Supplementary Figures



Supplementary Figure 1. Choice was mainly correlated with the difference in reward values of the two targets in terms of income. (**A–D**) Plotted are the correlations between selection of the left target and estimated income values of the left (A) and right (B) targets, and their sum (C) and their difference (D) for different values of τ and a specific value of Δ_n (indicated with an arrow in the inset) for monkey 1. The inset in each panel shows the correlation between choice and the corresponding income values of targets for different values of τ and Δ_n. (**E–H**) The same as in A-D but for monkey 2.



Supplementary Figure 2. Correlation between the MIB and estimated income of the chosen and unchosen targets. (**A**–**D**) Plotted are the correlations between the MIB and estimated income values of the chosen (A) and unchosen (B) targets, and their sum (C) and their difference (D) for different values of τ and a specific value of Δ_n (indicated with an arrow in the inset) for monkey 1. The inset in each panel shows the correlation between the MIB and the corresponding reward values (in terms of income) for different values of τ and Δ_n. (**E**–**H**) The same as in A-D but for monkey 2.