

Correspondence

# Reward creates oculomotor salience

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Theories of animal approach behaviour suggest that reward can create low-level biases in perceptual and motor systems, potentiating the processing of reward-associated environmental stimuli and causing animals to instinctively orient the head and eyes toward these objects [1]. However, the idea that reward can have this kind of direct impact on subsequent oculomotor processing has never been robustly tested, and existing research has largely confounded low-level effects with those mediated by strategy and attentional-set [2]. Here we demonstrate in humans that saccade trajectories are disrupted by a reward-associated distractor even when participants expect this object, know where it may appear, and do their best to ignore it. The reward history of a visual object thus has a direct, low-level, and non-strategic influence on how we deploy our eyes.

Prior research on the role of reward in oculomotor programming has largely relied on experimental designs in which neural or oculomotor responses to reward-predictive stimuli are examined [3]. This type of design does not allow for the distinction between a direct impact of reward and an influence mediated by strategy. Humans and other animals tend to look out for objects that provide information about upcoming reward [4], and this kind of attentional set is known to enhance visual and oculomotor responses [5]. Oculomotor bias toward reward-predictive stimuli thus is likely to reflect a strategic, indirect influence of reward feedback, mediated by attention, rather than the low-level, non-strategic priming proposed by theory.

Here we test whether a visual object's reward history has an impact on saccadic trajectory that is independent of strategy, and even in spite of it. We measured eye movements in eighteen healthy humans while they completed a saccadic selection task. This involved orienting the eyes from a central

fixation point to a target located at either the top center or bottom center of a computer screen. In every trial a task-irrelevant distractor was presented slightly to the left or right of the direct path between fixation and the target (see Figure 1A). The distractor could be red with the target green, or vice versa, and this was randomly determined for each trial. Participants knew that stimuli at the distractor locations must be ignored and that the colors of the target and distractor were task irrelevant.

Prior research with this type of display has shown that the distractor will cause target-directed saccades to deviate from their normal path, curving toward the distractor when the saccade is initiated quickly and away when it occurs later in time [6]. This time-course of deviation is thought to reflect the development of a spatially-specific inhibitory response to distractor salience, and saccadic deviation is accordingly used as a behavioural metric of salience in the oculomotor system [7].

When participants correctly deployed their eyes to the target they received a reward, either 1 or 10 points, with earnings for the experimental session determined by the number of accumulated points. Critically, reward magnitude was random: so long

as participants completed the task correctly, they were as equally likely to receive high-magnitude reward as low.

We expected that receipt of high-magnitude reward would potentiate subsequent processing of target features, increasing their relative salience [8]. Accordingly, when high-magnitude reward was received and the target and distractor colors swapped between trials, the distractor — now characterized by the color that defined the rewarding target in the immediately preceding trial — would have a stronger impact on the target-directed saccade. Trials were therefore binned based on two orthogonal experimental dimensions: whether the immediately preceding trial had garnered high or low-magnitude reward, and whether the target and distractor colors had swapped between trials (see Figure 1A). We also separated trials into short latency, mid latency, and long latency conditions, reflecting the speed with which the saccade was initiated after stimulus onset (for details see the Supplemental Information available on-line with this issue).

Figures 1B, 1C and 1D illustrate the saccadic deviation observed per experimental condition in each of the latency bins. Targets could be in the upper or lower visual hemifield, and

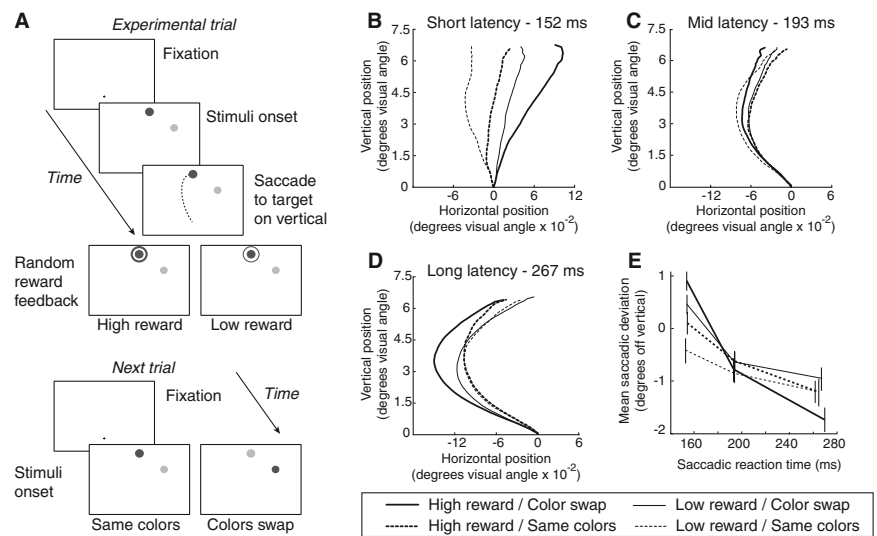


Figure 1. Experimental paradigm and results.

(A) Paradigm schematic. Target and distractor could be presented in red or green color; these differences in color are denoted here by shading. (B) Short latency, (C) mid latency, and (D) long latency saccadic trajectories, with horizontal scale magnified. These plots are in reference to a target in the upper hemifield and distractor in the right upper quadrant. (E) Mean angular deviation from a direct path between fixation and target for each condition and latency bin. Positive saccadic deviation values on the y-axis indicate curvature toward the distractor. Error bars reflect within-subject 95% confidence intervals.

distractors to the left or right, but these rectified plots are collapsed across stimuli locations and are in reference to a target in the upper hemifield and distractor in the right upper quadrant.

Short latency target-directed saccades in the high-reward / color swap condition (illustrated by the thick solid line in Figure 1B) are clearly drawn more closely to the distractor than saccades in the high-reward / same colors condition ( $P = 0.029$ ). In contrast, long latency target-directed saccades (illustrated by the thick solid line in Figure 1D) clearly deviate further away ( $P = 0.036$ ). For the purposes of numeric and statistical analysis we calculated a metric of saccade eccentricity based on mean angular deviation from a straight path between fixation and target [6]. These values are illustrated in Figure 1E and reiterate the pattern (see Supplemental Information for extended statistics).

Further analysis revealed: first, that the eyes were more likely to be erroneously deployed to the distractor location in the high-reward / swap condition than in the other conditions (3.6% vs. 2.5% of total eye movements); second, that target selection was less accurate in the high-reward / swap condition than in other conditions when saccades were quickly initiated, but became better when time passed between stimulus onset and saccadic execution; and third, that saccadic flight time was consistently longer in the high-reward / swap condition (Supplemental Figures S1A, S1E, S1F and Supplemental Results). A control experiment verified that the data pattern was created by the value of feedback stimuli, not physical differences in ring size (Supplemental Discussion).

The reward-associated distractor thus drew fast target-directed eye movements during saccadic flight, repulsed slow target-directed eye movements, made target-directed saccades generally slower and in some cases less accurate, and was more likely to capture the eyes to its location. This pattern is strikingly similar to that observed when the salience of the distractor is physically manipulated by increasing its luminance [7]. This is not a strategic effect: our participants knew to ignore objects at the distractor locations and that the colors of target and distractor were task irrelevant. There was no motivation or possibility for them

to establish an attentional set for a specific color.

Reward - and its neurological correlate in the dopaminergic midbrain - is thought motivate adaptive approach behaviour by driving humans and other animals to select, approach, and interact with objects similar to those that have garnered good outcome in the past [1]. The current results add to a growing literature suggesting that this type of reward-driven selection involves the action of low-level, non-strategic mechanisms that operate automatically [8–10]. Reward-associated stimuli draw our eyes, even when this is against our will.

#### Supplemental Information

Supplemental Information includes two figures and supplemental experimental procedures and can be found with this article online at \*bxs.

#### Acknowledgments

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## Supplemental Information: Reward creates oculomotor salience

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### Supplemental Methods

**Participants.** Twenty-one healthy students with normal or corrected-to-normal vision completed the experiment. Three were excluded from data analysis, two due to high error rate ( $>2$  SD from the mean) and one due to a difficulty maintaining a reliable pupil fix with the eye-tracking equipment. Six of the remaining 18 participants were male, three were left handed, and mean age was 23.6 years ( $\pm 3.7$  years SD). The experiment took approximately 1 hour to complete and participants were compensated between €8.00 and €9.00.

**Experimental Design.** Each participant completed at least 30 practice trials before 576 experimental trials in 24 blocks. Stimuli were presented on a CRT monitor with a 100 Hz. refresh rate located 70 cm from the eyes. All participants employed a chin-rest to maintain head position.

Participants began each trial by maintaining eye position within  $1^\circ$  visual angle of a central fixation mark ( $0.3^\circ$ ) and pressing a keyboard space bar. Following successful fixation the fixation mark reduced in size by  $0.1^\circ$  visual angle. After a further random interval of 300-600 ms the experimental stimuli appeared. Stimuli consisted of a larger circle ( $0.93^\circ$  visual angle diameter) presented  $7.38^\circ$  visual angle above or below the center of the screen and a smaller circle ( $0.80^\circ$  visual angle) located  $4.30^\circ$  vertical visual angle above or below fixation and  $3.60^\circ$  horizontal visual angle on the left or right (see Figure 1A). Stimuli locations were randomly determined for each trial with the confine that both stimuli always appeared together in the upper or lower hemifield. The larger circle was randomly green ( $x = 0.295, y = 0.541, 16.04$  cd/m<sup>2</sup>) with the smaller circle red ( $x = 0.550, y = 0.332, 11.89$  cd/m<sup>2</sup>) or vice versa. Display background was gray ( $x = 0.273, y = 0.294, 22.15$  cd/m<sup>2</sup>). If participants pressed the space bar prior to fixating the central mark the trial would not begin and an auditory tone indicated the error.

Participants were instructed to make an eye movement to the larger circle on the vertical meridian of the display. Saccades were considered target-directed when the eyes stayed within a  $36^\circ$  wedge beginning at fixation and centered on a straight line path to the target. Distractor-directed saccades were defined as eye movements that stayed within a similar wedge centered on the straight line path to the distractor. Eye movements that were neither target- nor distractor-directed were discarded

from analysis, as were saccades that began sooner than 100 ms after stimuli onset, later than 800 ms post-stimulus, or had a flight duration of more than 120 ms.

Participants received reward feedback 100 ms after each correct target selection. Reward feedback was presented for one second and was denoted in the thickness of a ring that appeared around the target: a thick ring ( $0.31^\circ$  visual angle) indicated the receipt of 10 points and a thin ring ( $0.06^\circ$  visual angle) indicated the receipt of 1 point. The ring was of the same color as the target and the total diameter of target and ring was  $1.85^\circ$  visual angle. Each point had a cash value of €0.00275 and participants were compensated based on the number of points accumulated through the experiment. Incorrect deployment of the eyes to any location other than the target resulted in the loss of 10 points, which was indicated by an auditory tone and the presentation of '-10' at the center of the screen for 1000 ms.

Participants were informed of the relationship between ring size and reward outcome, but to ensure that this relationship was clear reward outcome was additionally made explicit during practice trials (ie. '+10' or '+1' was presented slightly above or below the target).

Feedback at the end of each block reported average saccadic latency and number of points accumulated for that block, as well as the cash value of points accumulated thus far in the experiment.

**Eye movement tracking and data analysis.** Eye movements were measured using a tower-mounted Eyelink 1000 infrared video eye tracker (SR Research, Ontario, Canada) focused on the left pupil. Participants calibrated the tracker at the beginning of the experiment and after each break by fixating nine targets presented randomly in a 3x3 grid spanning the display. The calibration was additionally refined at the beginning of each trial with the center of the screen established as the point of fixation when participants pressed the space bar. Saccade onset was defined as the moment at which an eye movement exceeded an angular velocity of  $35^\circ/\text{s}$  or an acceleration of  $9500^\circ/\text{s}^2$ .

Figures 1B, 1C, and 1D illustrate the average saccadic path observed in each of the experimental conditions. The eye-tracker sampled at 1 kHz, but variation in saccadic flight time meant that saccades could be represented by unequal numbers of samples. We therefore calculated 70 evenly-spaced values based on linear interpolation of each eye movement. Saccadic paths illustrated in the figures reflect the mean average of these interpolated x and y coordinates.

To examine target-directed eye movements as a function of saccade latency the results from each experimental condition were additionally sorted into tertiles. Approximately 131 target-directed saccades were observed for each subject in each of the four conditions [HR/Swap 133 (9.6 SD); HR/NoSwap 131 (9.0 SD); LR/Swap 132 (9.0 SD); LR/NoSwap 130 (11.6 SD)]. These were partitioned into three equal bins for each participant such that the bins reflect short-latency saccades (Figure 1B), mid-latency saccades (Figure 1C), and long-latency saccades (Figure 1D). When

the number of trials was not evenly divisible by three, tertiles were created such that the long-latency bin could contain one or two more trials than the others.

For the purposes of numeric and statistical analysis we calculated mean angular deviation of each saccade from a straight-line path between fixation and target (an approach described and detailed in Appendix 1 of [S1]). These values were mean averaged across all saccades in each condition and across subjects, garnering the results illustrated in Figure 1E.

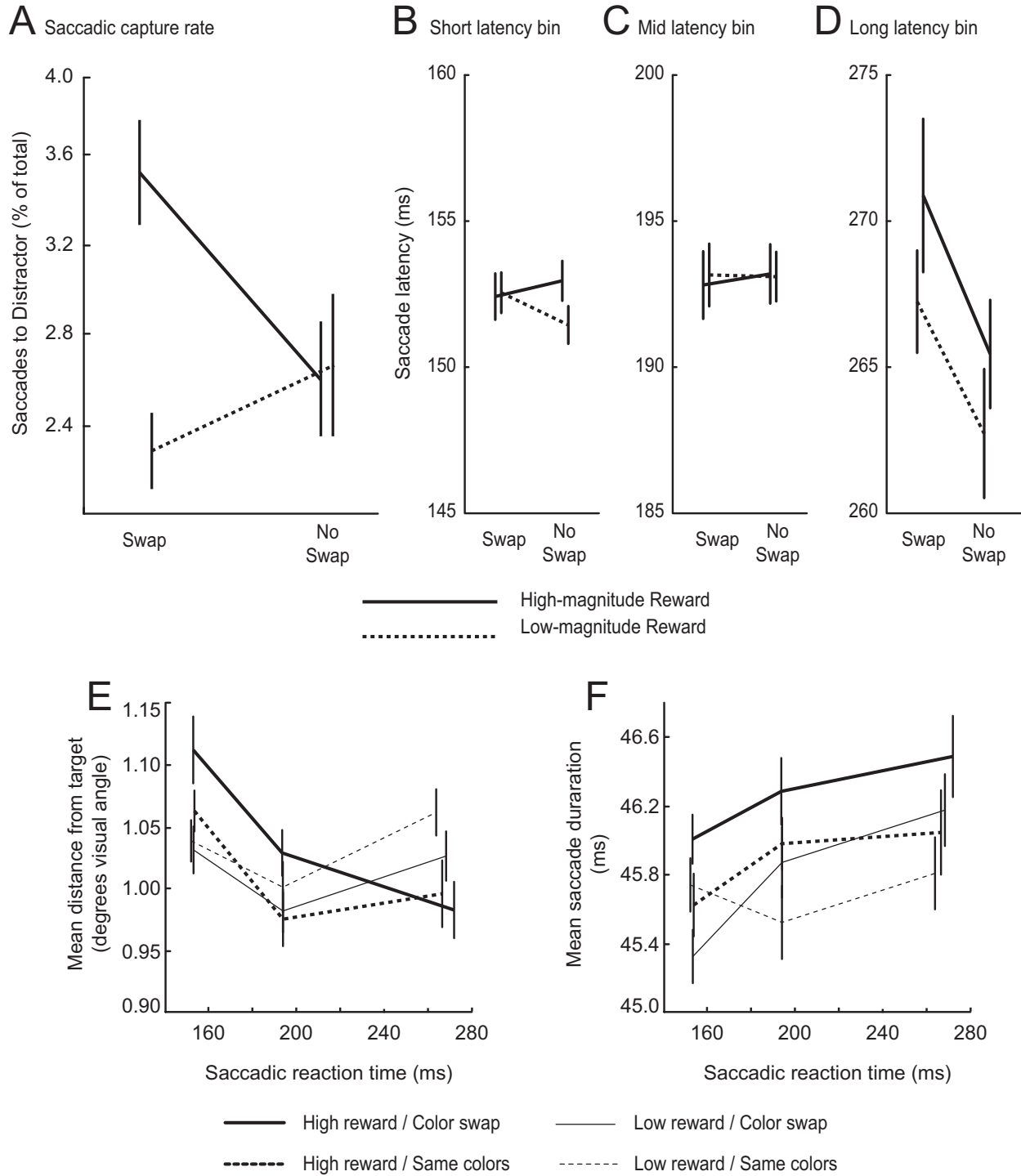
Error bars in Figure 1E and Supplemental Figures reflect within-subject 95% confidence intervals [S2].

### Supplemental Results

**Saccadic Deviation.** Statistical analysis began with an omnibus repeated measures analysis of variance (RANOVA) of saccadic deviation. This analysis had factors for prior reward (high-magnitude vs. low-magnitude), latency bin (short vs. long), and color swap (swap vs. no swap). Note that analysis is limited here to results from the short and long latency bins in order to remove the need for consideration of data sphericity. The RANOVA revealed a significant main effect of latency bin [ $F(1,17) = 15.372, p < 0.001, \eta_p^2 = 0.475$ ], a significant interaction between latency bin and reward [ $F(1,17) = 5.374, p = 0.033, \eta_p^2 = 0.240$ ], and a significant interaction between latency bin and color swap [ $F(1,17) = 6.743, p = 0.019, \eta_p^2 = 0.284$ ; color swap:  $F(1,17) = 2.624, p = 0.124$ ; reward x color swap:  $F(1,17) = 2.011, p = 0.174$ ; reward x color swap x latency bin:  $F(1,17) = 1.04, p = 0.321$ ; reward:  $F < 1$ ]. A follow-up RANOVA limited to the short latency bin with factors for prior reward and color swap revealed main effects for each factor [prior reward:  $F(1,17) = 5.617, p = 0.030, \eta_p^2 = 0.248$ ; color swap:  $F(1,17) = 9.246, p = 0.007, \eta_p^2 = 0.352$ ] but no interaction [ $F < 1$ ]. A similar follow-up RANOVA limited to the long latency bin revealed no main effects [prior reward:  $F(1,17) = 2.429, p = 0.138$ ; color swap:  $F < 1$ ] but a significant interaction [ $F(1,17) = 4.82, p = 0.042, \eta_p^2 = 0.247$ ].

Our primary interest lay in the effect of reward on saccadic deviation in color swap trials, and we accordingly conducted an additional follow-up RANOVA based on results from color swap trials with factors for prior reward and latency bin. This revealed a significant main effect of bin [ $F(1,17) = 16.541, p < 0.001, \eta_p^2 = 0.493$ ], reflecting a change from deviation toward the distractor in short latency trials to deviation away in long latency trials, and an interaction between bin and reward [ $F(1,17) = 7.762, p = 0.013, \eta_p^2 = 0.313$ ], driven by greater deviation toward the distractor following the receipt of high-magnitude reward when saccadic latency was short but greater deviation away when saccadic latency was long. There was no main effect of reward [ $F(1,17) = 1.041, p = 0.322$ ].

Planned contrasts confirmed that in short latency trials the eyes deviated further toward the distractor in the high reward / swap condition than the low reward / swap condition [ $t(17) = 2.374, p = 0.029, \text{Cohen's } d = 0.560$ ], but that in long latency trials the eyes deviated further away from the distractor in the high reward / swap



Supplemental Figure 1. (A) Short, (B) mid, and (C) long saccadic latencies per experimental condition. (E) Saccadic accuracy per condition, as reflected in the distance between saccadic endpoint and target stimulus center. (F) Saccadic duration per condition. Error bars here and below reflect within-subject 95% confidence intervals.

condition than the low reward / swap condition [ $t(17) = 2.277$ ,  $p = 0.036$ , Cohen's  $d = 0.536$ ].

**Saccadic capture.** As illustrated in Figure S1A, participants were more likely to misdirect their eyes to the distractor in the high reward / color swap condition. Statistical analysis of saccadic capture rate demonstrated the reliability of this pattern: a RANOVA with factors for color swap and prior reward revealed a trend towards a main effect of reward [ $F(1,17) = 3.381$ ,  $p = 0.083$ ,  $\eta_p^2 = 0.166$ ], no effect of color swap [ $F(1,17) = 1.046$ ], but, critically, a significant interaction between reward and swap [ $F(1,17) = 5.415$ ,  $p = 0.033$ ,  $\eta_p^2 = 0.242$ ]. A planned contrast of the saccadic capture rate in the high reward / swap condition (3.6%) to pooled results from the other three conditions (2.5%) was significant [ $F(1,17) = 10.396$ ,  $p = 0.005$ ,  $\eta_p^2 = 0.3778$ ].

**Saccadic Onset Latency.** Figure panels S1B, S1C, and S1D present saccadic latencies per experimental condition and latency bin. Long latency saccades appear slower when target and distractor colors swapped between trials. Consistent with this, a RANOVA based on saccadic latency with factors for color swap (swap vs. no swap), prior reward, and latency bin (short vs. mid vs. long) revealed a marginally significant interaction between latency bin and color swap [ $F(1,17) = 4.188$ ,  $p = 0.045$ ,  $\eta_p^2 = 0.198$ ] alongside a trivial effect of latency bin [ $F(2,34) = 124.580$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.880$ ]. Apparent slowing following the receipt of high-magnitude reward did not prove reliable [reward:  $F(1,17) = 1.638$ ;  $p = 0.218$ ,  $\eta_p^2 = 0.088$ ; latency bin x reward:  $F(2,34) = 1.299$ ; color swap:  $F(1,17) = 1.508$ ; all other  $F_s < 1$ ].

**Saccadic Accuracy.** To determine the impact of a reward-associated distractor on the accuracy of target-directed eye movements we measured the distance of each saccade endpoint from the center of the target. Results from this analysis are presented in Figure S1E. The accuracy of short-latency saccades in the high-reward / color swap condition is worse than is observed in other conditions, as evident in a greater endpoint distance from target center, but performance in this condition improved when saccades were initiated later in time.

To test this pattern we conducted a RANOVA with factors for latency bin (short vs. mid vs. long), prior reward (high vs. low), and color swap (color swap vs. no swap). This revealed a significant three-way interaction [ $F(2,32) = 4.000$ ,  $p = 0.028$ ,  $\eta_p^2 = 0.190$ ; reward:  $F(1,17) = 2.644$ ,  $p = 0.122$ ,  $\eta_p^2 = 0.135$ ; latency:  $F(2,34) = 1.185$ ,  $p = 0.318$ ,  $\eta_p^2 = 0.065$ ; latency x color swap:  $F(2,34) = 1.420$ ,  $p = 0.256$ ,  $\eta_p^2 = 0.077$ ; all other  $F_s < 1$ ]. A follow-up RANOVA limited to the swap condition with factors for latency bin and prior reward revealed a marginally significant interaction [ $F(2,34) = 2.753$ ,  $p = 0.078$ ,  $\eta_p^2 = 0.139$ ; reward:  $F(1,17) = 2.339$ ,  $p = 0.145$ ,  $\eta_p^2 = 0.121$ ; latency bin:  $F(2,34) = 1.182$ ,  $p = 0.319$ ,  $\eta_p^2 = 0.065$ ].

We interpret this as evidence of increased salience of the distractor in the high-reward / color swap condition. Rapidly executed eye movements are drawn to the distractor location, adversely impacting subsequent target selection. However,

when time passes between stimulus onset and the beginning of the saccade, participants are afforded the opportunity to suppress distractor salience and accuracy improves.

**Saccade Duration.** We analyzed saccadic flight times to determine the impact of a reward-associated distractor on the duration of target-directed eye movements. Results are presented in Figure S1F. Flight time was consistently longer in the high-reward / color swap condition across all latency bins.

To test this pattern we conducted a RANOVA limited to the swap condition with factors for latency bin (short vs. mid vs. long) and prior reward (high vs. low). This revealed a main effect of reward [ $F(1,17) = 5.554$ ,  $p = 0.031$ ,  $\eta_p^2 = 0.246$ ; all other  $F_s < 1$ ].

The reward-associated distractor thus increased the time required for the eyes to be deployed from fixation to the target. This is consistent with the fact that saccadic paths were longer in this condition due to increased curvature towards the distractor in short-latency saccades and away in long-latency saccades. It took the eyes more time to travel a longer path.

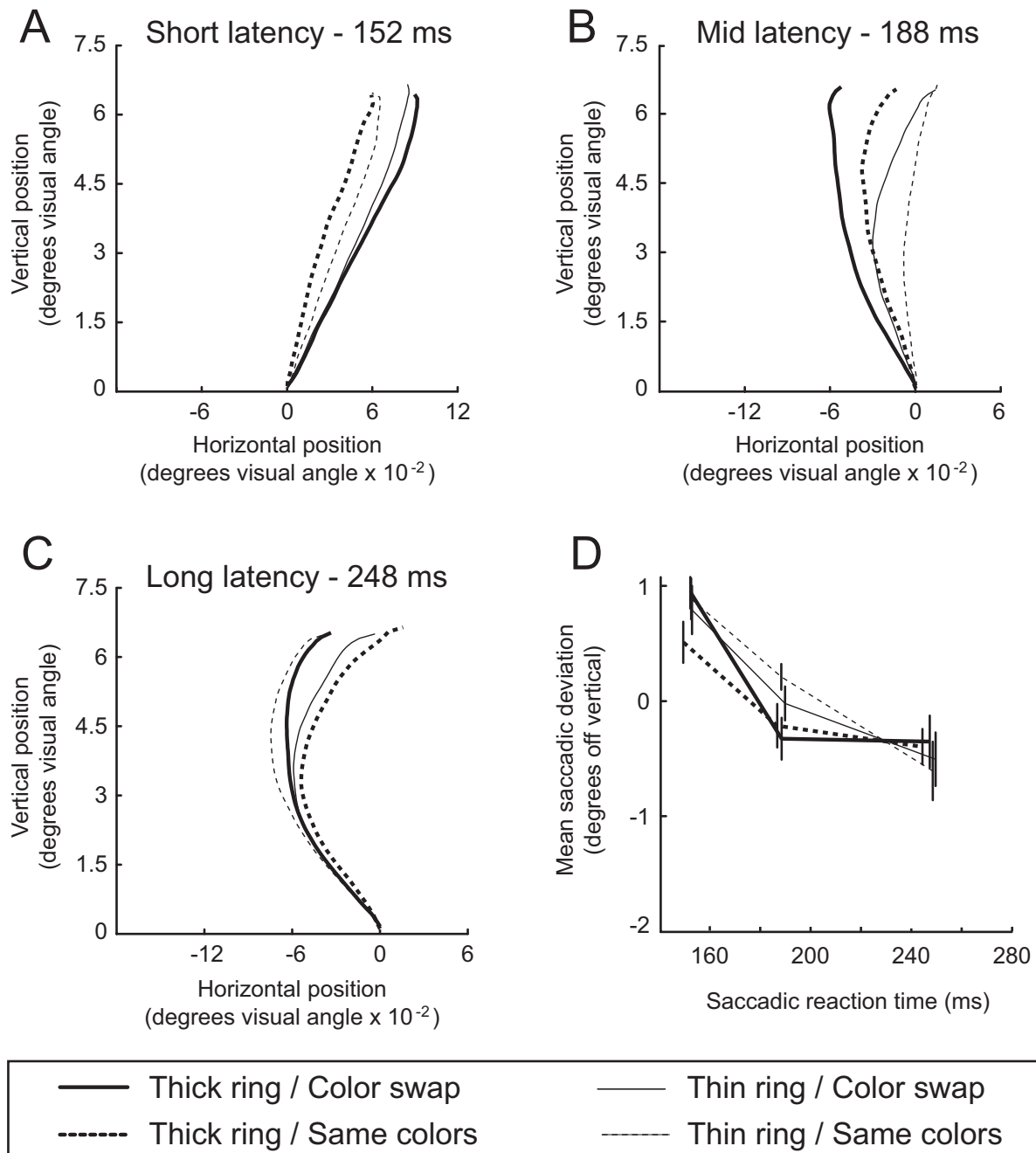
Note that while raw degrees of freedom are presented in all statistical tests above, p-values reflect calculations based on Greenhouse-Geisser corrected degrees of freedom where appropriate.

### **Supplemental Discussion**

As evident in Figure 1C, the deviation of mid-latency saccades is roughly equivalent in all four experimental conditions. This is consistent with the idea that the reward associated distractor initially draws the eyes and later repulses them. This account necessitates that there be a point in time where attractive and repulsive biases reach equilibrium: the distractor has been suppressed to the degree that it no longer draws the eyes, but has not yet been suppressed to the degree that it repulses them. This equilibrium appears to have been reached in the mid-latency results, creating equivalency across conditions.

We would like to point out that results from this experiment may be specific to the association of reward with color. Overt visual search for color stimuli is in fact more efficient than search for stimuli defined by other features. For example, color-defined targets will more quickly and accurately draw the eyes [S3,S4], and intertrial priming of uniquely colored target is larger and more robust than that of targets defined by other visual features [S5]. We have suggested elsewhere that these increases in priming may be related to the size of neural receptive fields, with the relatively large size of colour receptive fields resulting in increased ambiguity in visual representation, and thus increased need for the selective mechanisms that create intertrial priming [S6]. Given these characteristics of search and priming, there is the clear need for dedicated research to determine if the association of reward to other visual features has a corresponding impact on saccadic eye movements.





*Supplementary Figure 2. Results from control experiment. Saccadic paths in (A) short, (B) mid, and (C) long latency bins. As in the primary experiment these plots are in reference to a target in the upper hemifield and a distractor to the right of the vertical meridian.*

**Control Experiment.** In the primary experiment reward feedback was denoted via the width of a ring presented around the target after it had been fixated. This ring had the same color as the target and thus introduced a sensory confound: when feedback indicated the receipt of high-magnitude reward, the large, target-colored ring may have primed the target color in subsequent trials, benefitting subsequent visual processing of objects with this color.

We conducted a control experiment to test this possibility. The control was identical to the primary experiment with one exception: there was no manipulation of reward. No points were accumulated during experimental participation and participants were compensated for their time at a fixed rate. A thick or thin ring continued to be presented at the end of each trial, but the width of this ring was randomly determined and had no meaning to the participants, who were instructed to ignore it.

Sixteen healthy participants with normal or corrected-to-normal vision completed the control experiment. None had taken part in the primary experiment. Two were excluded from data analysis, one due to high error rate (>2 SD from the mean) and one due to a difficulty maintaining a reliable pupil fix with the eye-tracking equipment. Four of the remaining 14 participants were male, 1 was left handed, and mean age was 22.0 years (+/- 3.1 years SD). The experiment took approximately 1 hour to complete and participants were compensated either financially (€9.00/hour) or with course research credit.

Figure panels S2A, S2B, and S2C illustrate saccadic results as a function of ring size, color swap, and latency bin. There is no evidence of the pattern identified in the primary experiment: short-latency target-directed saccades in the thick-ring / swap condition do not show any particular bias towards the distractor location, and nor do long-latency saccades show any particular bias away.

In order to statistically assess differences between the primary and control experiments we conducted a RANOVA. This was based on data from the color swap condition with a between-subject factor for experiment (primary vs. control) and within-subject factors for prior ring thickness (thin vs. thick; note that this conveyed meaningful information about reward in the primary experiment) and latency bin (short vs. long). A main effect of latency bin was revealed [ $F(1, 30) = 32.789, p < 10^{-5}, \eta_p^2 = 0.522$ ], as was a critical interaction between experiment, latency bin, and prior ring thickness [ $F(1,30) = 4.342, p = 0.046, \eta_p^2 = 0.126$ ; reward x latency:  $F(2, 60) = 1.932, p = 0.175$ ; reward x experiment:  $F(1,30) = 1.214, p = 0.279$ ; all other  $F_s < 1$ ]. This three-way interaction reflects increased saccadic deviation toward the distractor in the swap condition in short-latency eye movements, and away in long-latency eye movements, following presentation of a thick ring - but only in the primary experiment.

A second RANOVA examined results from the control experiment in isolation. This had factors for latency bin and reward and revealed a main effect of latency bin [ $F(1,30) = 25.041, p < 10^{-4}, \eta_p^2 = 0.658$ ], but no main effect of reward and no

interaction [ $F_s < 1$ ]. In the control experiment there was thus no reliable saccadic deviation towards the distractor following presentation of the thick ring in short-latency eye movements or away from the distractor in long-latency eye movements.

The control experiment demonstrates that the biases of eye movements identified in the primary experiment are a product of the reward information conveyed by the feedback, not the concomitant change in physical stimulation.

Note that results from the primary experiment reflect data from 18 participants, whereas results from the control reflect data from 14 participants. Comparison between these datasets is accordingly sensitive to differences in group variance. We assessed the degree of heteroscedasticity using Levene's test of equality of error variance [S7]. This revealed no reliable differences in variance (all  $p$ s  $> 0.15$ ), suggesting that results from the comparison across experiments reflect valid statistical estimates.

### **Supplemental References**

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