

Effects of reward on oculomotor control

Brónagh McCoy and Jan Theeuwes

Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

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McCoy B, Theeuwes J. Effects of reward on oculomotor control. *J Neurophysiol* 116: 2453–2466, 2016. First published August 31, 2016; doi:10.1152/jn.00498.2016.—The present study examines the extent to which distractors that signal the availability of monetary reward on a given trial affect eye movements. We used a novel eye movement task in which observers had to follow a target around the screen while ignoring distractors presented at varying locations. We examined the effects of reward magnitude and distractor location on a host of oculomotor properties, including saccade latency, amplitude, landing position, curvature, and erroneous saccades toward the distractor. We found consistent effects of reward magnitude on classic oculomotor phenomena such as the remote distractor effect, the global effect, and oculomotor capture by the distractor. We also show that a distractor in the visual hemifield opposite to the target had a larger effect on oculomotor control than an equidistant distractor in the same hemifield as the target. Bayesian hierarchical drift diffusion modeling revealed large differences in drift rate depending on the reward value, location, and visual hemifield of the distractor stimulus. Our findings suggest that high reward distractors not only capture the eyes but also affect a multitude of oculomotor properties associated with oculomotor inhibition and control.

reward; oculomotor control; remote distractor; global effect

NEW & NOTEWORTHY

A novel eye movement task was used in which observers continuously followed a target around the screen. Distractors with different reward magnitude were presented along with the target. The eyes went more often to a high than low reward distractor. Reward magnitude also affected the global and remote distractor effect and saccade amplitude. Distractors in the opposite visual hemifield to the target resulted in more erroneous saccades than equidistant distractors in the same hemifield.

WHEN WE SAMPLE VISUAL INFORMATION from the world around us, we are constantly making saccadic eye movements. Between eye movements there are brief fixations when the image is relatively stable during which information is picked up. We are engaged in continuous eye movement sampling during most of our day when reading text, driving cars, viewing displays, and interacting with the world in general. Following a saccade, the fixation of an interesting target image may represent a rewarding experience. The experience of receiving a reward is a primary driver of motivated behavior among humans and animals alike (e.g., Pessoa and Engelmann 2010). In the laboratory, when studying eye movements we usually use discrete-trial sequences of events in which observers have to move their eyes back to the center of the display after each

saccade sequence (see for example the oculomotor capture paradigm; Theeuwes et al. 1998, 1999). In the current study, we investigated the effect of reward on oculomotor behavior by using a novel, continuous eye movement task in which observers had to follow a target around the screen. After each saccade, the next target appeared at a new location without the need to refixate at the center of the display. This continuous eye movement design ensured fast saccades, allowing the investigation of oculomotor control in a more realistic environment and eliminating the strong top-down component often seen in standard paradigms using a discrete-trials procedure.

It is well known that reward can improve motivation and learning (Thorndike 1911). When participants know that performing at an optimal level helps them earn additional (monetary) rewards, they are motivated to perform better, resulting in faster and more accurate responses. For example, Milstein and Dorris (2007) showed that observers make faster eye movements when they can obtain a reward; moreover, saccadic eye latencies were negatively correlated with the relative expected reward value of the target. Similarly, Bucker and Theeuwes (2014) showed that reward-induced motivation improved visual orienting and demonstrated that high reward-induced motivation increased top-down control in attentional cueing.

Recently, however, the effects of reward have also been implicated in tasks that are less susceptible to reward-induced motivation. Several studies have demonstrated that an object that is associated with obtaining a reward may be prioritized for selection in an automatic bottom-up fashion, independent of motivation (Anderson et al. 2011a, 2011b; Failing and Theeuwes 2014, 2016; Hickey et al. 2010; Jahfari and Theeuwes 2016). By examining eye movements, Theeuwes and Belopolsky (2012) showed that even when no rewards could be obtained anymore, observers made more eye movements to a distractor that was previously associated with high reward compared with one associated with low reward. In their study, observers made eye movements to either a vertical or horizontal bar appearing among shape stimuli, placed at equidistant clock positions on an imaginary circle. For each participant, depending on the orientation, a correct saccade to the vertical or horizontal bar led consistently to either a high or low monetary reward. In a subsequent separate test phase in which reward was no longer available, participants made an eye movement to one gray circle target appearing among red circles. On a subset of trials, an irrelevant vertical or horizontal distractor bar appeared with the onset of the target, at a previously unoccupied location. Theeuwes and Belopolsky found that as the training phase progressed, participants became quicker to initiate a saccadic eye movement to the target when it was associated with high reward compared with low reward, demonstrating a motivation-induced speeding up of

Address for reprint requests and other correspondence: B. McCoy, Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, 1081 BT Amsterdam, The Netherlands (e-mail: b.mccoy@vu.nl).

saccades. Crucially, however, during the following test phase, participants made significantly more eye movements to the previously high rewarded stimulus onset (horizontal or vertical bar) compared with the previously low rewarded stimulus, even when these distractors were no longer relevant for the task at hand (see also Hickey and van Zoest 2013). Further studies have demonstrated that eye movements are also made to distractors that signal the availability of reward on a trial, even when making an eye movement to the distractor instead of the target results in the loss of reward (Failing et al. 2015; Le Pelley et al. 2015).

The current study was designed to systematically investigate the effect of reward-associated distractors on oculomotor behavior. Saccadic eye movements are often used as a tool to help uncover the neural bases of reward choice. Two important brain areas involved in oculomotor processing are the lateral intraparietal area (LIP) and frontal eye field (FEF). These have projections to subcortical regions, including the basal ganglia (BG) and superior colliculus (SC). The initiation and execution of saccadic eye movements is controlled by the SC, with average responses of the entire population of active neurons determining the direction, amplitude, and velocity of a saccade (Lee et al. 1988; Schall 1991; Sparks and Mays 1981). Both LIP and FEF have spatial receptive fields and respond selectively to stimuli that attract attention (Bisley and Goldberg 2010; Thompson and Bichot 2005). Visual representation in LIP is rather sparse, with only very salient or behaviorally relevant objects strongly represented (Gottlieb et al. 1998). In primate research, when a monkey has to choose between two visually distinct objects that are each associated with different rewards, single-unit recording shows that the firing rates of neurons in LIP are proportional to the relative expected subjective value of the objects (Sugrue et al. 2004). The BG are needed for voluntary control of body movements, including saccadic eye movements (DeLong and Georgopoulos 1981). The caudate nucleus (CN), a structure within the BG, has also been associated with reinforcement learning, reward-based decision making, and the orienting of the eyes to rewarding stimuli (Hikosaka et al. 2006; Schönberg et al. 2007). The substantia nigra pars reticulata (SNr) of the BG plays an important role in selecting an appropriate action by releasing the tonic inhibition it holds over the SC, the final station before execution of an eye movement. Disinhibition of the SC by the BG is therefore suggested to occur via a CN-SNr-SC circuit (Gottlieb et al. 2014; Hikosaka et al. 2000).

The goal of the current study was to determine the extent to which distractors associated with reward affect oculomotor control in a continuous eye movement task. In different conditions, distractors associated with reward were presented simultaneously with the target at specific locations near or far from the target location, either within or across visual hemifield. The color of the distractor signaled the availability of the amount of reward available in each trial; however, participants were never explicitly informed of this color-reward contingency. By not informing participants of the association, the top-down component of immediately attending to the distractors was not available. This posed a more natural setting for learning from experience, targeting the concept of reward-learning and history effects in the framework proposed by Awh et al. (2012). Crucially, if participants made a saccade to the distractor, no reward was obtained on that trial. In other words,

participants had to suppress making a saccade to the distractor because doing so would have a negative impact on their total reward payment.

There are several classic eye movement effects that have been reported with the typical discrete-trial paradigm. We assessed how distractor-related reward contingencies affect these classic eye phenomena while using a continuous eye movement task. First, we examined the role of reward-associated distractors on the remote distractor effect (Walker et al. 1997). This effect demonstrates that distractors presented at remote locations increase saccade latency but have little effect on landing position. Second, we examined the global effect, which implies that distractors presented in close spatial proximity to the target modulate the landing position while having little effect on saccade latency (Coren and Hoenig 1972; Findlay 1982). Third, we investigated errors in oculomotor control, referred to as oculomotor capture (Theeuwes et al. 1998, 1999), representing those trials in which observers make saccades toward the distractor instead of the target. These erroneous saccades are assumed to occur in a bottom-up, automatic fashion, against the intentions of the observer (Meeter et al. 2010). Fourth, we examined how reward-associated distractors affected saccade deviations. It is known that depending on the condition, saccades may deviate either toward or away from distractors (see Van der Stigchel and Theeuwes 2005). Fifth, we wanted to establish the specific role of distractors when presented equidistant within and across hemifields. It is well known that the neural representation of a target is diminished by the presence of nearby distractors (Reynolds et al. 1999). Stimuli presented simultaneously are not processed independently but compete for neural representation in a mutually suppressive way (Chelazzi et al. 1998; Hickey and Theeuwes 2011; Torralbo and Beck 2008). Finally, we determined whether the effects of reward could be fitted by means of a Bayesian hierarchical drift diffusion model, allowing us to determine how reward value and distractor location are represented by saccade latencies and erroneous behavior in a probabilistic framework.

MATERIALS AND METHODS

Participants

Twenty-four students of the Vrije Universiteit Amsterdam (age 24.8 ± 3.8 yr, mean \pm SD) with reported normal or corrected-to-normal vision gave written informed consent to take part in the study. The experiment was approved by the Scientific and Ethical Review Committee of the Vrije Universiteit Amsterdam. The sample included 8 males (age 26.0 ± 5.3 yr) and 16 females (age 24.3 ± 2.8 yr). Participants were given fixed monetary compensation of 9 euros for undergoing eye tracking and received a reward bonus of up to 9.90 euros (7.27 ± 0.93 euros) based on their performance during the task.

Apparatus

The experiment and stimuli were created using OpenSesame software for Windows (Mathôt et al. 2012), based on a PsychoPy backend. Stimuli were presented on a Lacie electron22 blueIV monitor ($1,024 \times 768$ resolution, 100-Hz refresh rate), with viewing distance held constant at 60 cm using a chin rest. Participants were tested in a sound-attenuated, dimly lit room. Eye movements were recorded using an EyeLink 1000 Tower Mount eye tracker (SR Research, Kanata, ON, Canada) with 1,000-Hz temporal resolution

and $<0.01^\circ$ gaze resolution. An automatic algorithm detected saccades using minimum velocity and acceleration criteria of $35^\circ/\text{s}$ and $9,500^\circ/\text{s}^2$, respectively. Data were collected and analyzed for the right eye only.

Stimuli

Participants had to follow a black unfilled target circle (0.8° radius) around the screen (gray background, CIE coordinates: $x = 0.313$, $y = 0.329$; 55.834 cd/m^2) while ignoring a salient unfilled colored distractor circle of the same size. The distractor during the practice session was red (CIE coordinates: $x = 0.501$, $y = 0.347$; 28.20 cd/m^2). During the task, the distractor color was either blue (CIE coordinates: $x = 0.190$, $y = 0.200$; 28.30 cd/m^2), green (CIE coordinates: $x = 0.265$, $y = 0.490$; 27.70 cd/m^2) or orange (CIE coordinates: $x = 0.480$, $y = 0.465$; 27.70 cd/m^2).

Task Design

Calibration of the eye tracker was carried out at the beginning of each participant's session. The calibration procedure tested participants' gaze positions for nine fixed locations on the screen, to ensure accurate tracking of the eyes. Participants first completed a practice block of the experimental task consisting of 75 trials. The block began with drift correction at the center of the screen. Drift correction is an automatic procedure carried out by the eye tracker to make sure an observer's eyes have not "drifted" far from the center (as a result of head motion, for example), making the original calibration no longer valid. If the drift correction error is too large, the experimenter is prompted to recalibrate before proceeding. After a variable interval (50–250 ms), a target (black circle) appeared at a position on an imaginary circle with an eccentricity of 4.5° visual degrees. A red distractor circle appeared simultaneously with the target, also at this eccentricity. The distractor could take one of three positions relative to the target: at a clockwise polar angle of 30° , 120° , or 180° . Participants were instructed to make a quick saccade to the target circle. During the practice, the cutoff time for the eye to land at the target was 2,000 ms. This was reduced in the experimental task for each participant, depending on their individual saccade latency (the time between stimulus onset and initiation of a saccade) during the practice session. Since people have different baseline eye movement latencies, the 85th percentile of each participant's unique saccade latency distribution was taken after the practice block and used as a latency cutoff for subsequent experimental trials so that participants would continue making quick saccades throughout the experiment. Although ensuring fast saccades, the 85th percentile is not too strict, allowing the vast majority of saccades to be considered in time. This method of accounting for differences in baseline latencies has been used in previous similar experiments (Bucker et al. 2015; Le Pelley et al. 2015). Correct trials were those made to the target region of interest (1.6° visual degrees; twice the radius of the stimulus) within the cutoff time. If a first saccade was made to the distractor region of interest (within 1.6°), a sinewave 50-ms beep was heard, signaling an incorrect trial. Once the trial was completed the next trial began with the previous target black circle as the new starting point, presented alone on the screen for a random interval of 50–250 ms. Before each trial began, it was necessary for the eye to be within the previous target (new starting point) region of interest. This constituted the continuous nature of the design. After the practice session, participants completed the experimental task of 1,800 trials, split into 20 short blocks of 90 trials each. Each block began with central fixation and drift correction. Trials in the main experiment followed the same procedure as in the practice, with the additional element of reward association; see Fig. 1 for the trial sequence and timings.

Each trial contained a distractor that led to feedback of high reward (10 points), low reward (1 point), or no reward associated with the color of the distractor. The blue, green, and orange distractor colors

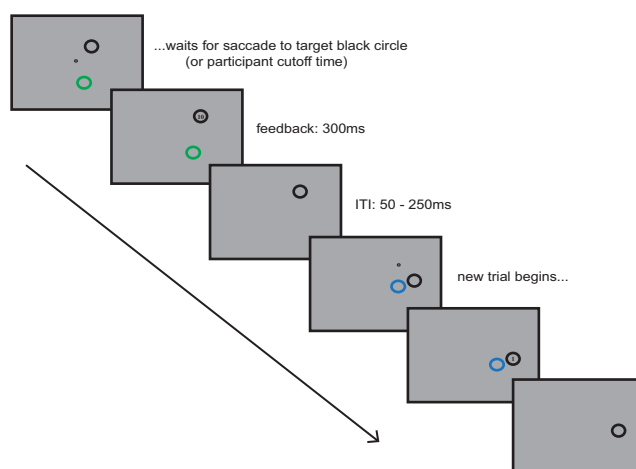


Fig. 1. Trial sequence. Participants made a saccade to the target black circle, following it to the next location in every trial. In each trial a colored distractor also appeared. Once a correct saccade to the target was made, feedback was presented (10, 1, or 0 points). An intertrial interval of 50–250 ms was followed by a new trial. The small black dots are shown for illustration purposes only, to indicate the starting point for each trial. Participants continuously made an eye movement from one black circle to the next across trials. Sizes are not to scale; they are enlarged for clarity.

were counterbalanced for reward level across participants. When a participant made a correct saccade to the target, feedback was presented for 300 ms within the target circle as a "10" or "1" (size 1.08° visual angle) or else nothing appeared, indicating no reward. Participants were not informed of the distractor color-reward association. Importantly, if an incorrect saccade was made to the distractor, a beep was heard and no reward was received for that trial. If participants were slower than the cutoff time, an "s" (1.08°) appeared in the target circle. The end of feedback presentation constituted the end of the trial, and the next trial began in the same way as during practice. Each trial therefore required one saccade to the next target, with the presentation of feedback ending the trial. Figure 2 shows examples of conditions used in the experiment: three possible distractor colors and three distractor positions relative to the target (only the stimulus presentation screens are shown). All combinations of these colors and positions made up the full set of conditions in the experiment. To ensure that the target and distractor did not end up in positions off the screen, a template of possible target positions was created. This took on a lattice structure, with target positions located on one of the four main diagonals from the starting point of each trial (45° , 135° , 225° , or 315° polar angle), always at 4.5° eccentricity. At the end of each block, participants received feedback on mean reaction time and points received for that block. At the end of the experiment, their total accumulated points were converted into money and displayed on the screen [(points/1,000) \times 1.50 euros].

Data Analysis

Data were processed and analyzed using Data Viewer (version 2.3.1; SR Research), Python (version 2.7), and SPSS software (version 23.0; SPSS, Chicago, IL). Trials from the practice session were excluded, and the following properties of all first eye movements in the experimental session were analyzed: saccade latency, erroneous saccades toward the distractor, saccadic amplitude and landing position, and curvature toward the distractor. Saccade latency was described as the time interval between the simultaneous presentation of the target and distractor and the initiation of the saccadic response. Data were analyzed for first saccades, containing no blinks, which started from within 1.6° of the starting point of each trial (twice the circle radius) and landed within 1.6° of the target or distractor circle. Saccade latencies less than 80 ms (anticipation errors) and greater



Fig. 2. Trial conditions. For each participant, each distractor color signaled the availability of either high, low, or no reward for that trial. Distractors could be placed at either 30, 120, or 180 polar degrees from the target. All distractor location-reward combinations appeared equally often for each participant. Sizes are not to scale. The small black dot never appeared in the experiment; it is shown to illustrate the starting point of the trial.

than each participant's individual cutoff time (see *Task Design*) were excluded from further analysis. If there was any erroneous drift of the eyes within a block, resulting in a portion of hanging trials (in which the script could not allocate the eye as being at either the target or distractor location), then that block of trials was omitted from further analysis. Unless otherwise stated, variance in all analyses is reported as standard error of the mean (SE).

Latency quartiles. Latency quartiles were calculated for erroneous saccade trials for each individual participant. The percentage of those erroneous trials was calculated per reward condition, taking quartiles from each participant's unique saccadic latency distribution across each reward condition. Thus percentages of erroneous saccades to high-, low-, and no-reward distractors were calculated for the fastest 25%, 25–50%, and 50–75% and the slowest 25% of saccade latencies.

Global effect. The midpoint between the target and distractor centers was taken for all 30° trials. The absolute distance from this point to the landing position of a correct eye movement to the target was expressed as a percentage representing landing closer to or further from the midpoint (positive or negative, respectively) with respect to the center of the target.

Saccadic curvature. Saccadic curvature was analyzed by taking all correct first saccades to the target which contained more than 10 samples, i.e., saccades lasting longer than 10 ms. The “main sequence” linear relationship between saccade magnitude and duration (Bahill et al. 1975) predicts that correct saccades in this task, with an amplitude of $\sim 4.5^\circ$, should last longer than this duration. The calculation of saccadic curvature was based on the peak deviance method (Doyle and Walker 2001; Nummenmaa and Hietanen 2006; Smit and Van Gisbergen 1990). The angular deviation of the saccade path for each 1-ms sample was calculated relative to a straight line from the starting point of the saccade to the saccade endpoint. The sample with the maximum angular deviation (in either a positive or negative direction) was taken as the peak angle. The perpendicular distance from this sample point to the straight line joining the start and end point of the saccade was deemed the peak deviance P . The curvature C was thus calculated by dividing the peak deviance P by the distance of the straight line from the saccade start to end point, otherwise known as the amplitude A (i.e., $C = P/A$). This correction for amplitude was necessary to account for differences in curvature for given differences in amplitude (Smit and Van Gisbergen 1990). The curvature was then expressed as a positive (toward the distractor) or negative (away from the distractor) unitless entity.

Visual hemifield. We analyzed the special case of hemifield given a fixed target-distractor distance, i.e., those trials in which the distractor was presented at 120° from the target. Of all 120° distractor trials, approximately half were ipsilateral and half were contralateral to the

target. The physical distance between the target and distractor was the same for ipsilateral and contralateral trials (see Fig. 3 for an example of ipsilateral and contralateral distractor trials).

Hierarchical drift diffusion modeling. Drift diffusion modeling (DDM) was also carried out on the data. This technique has been used extensively to explain behavioral data in choice experiments involving two competing items (Ratcliff and Rouder 1998, 2000). Since eye movements to a target in the presence of a distractor require a motor plan to the target location while inhibiting a competing location, tasks of this nature may be described as a speeded decision process at a fundamental level. The DDM is a sequential sampling method that assumes decisions are made by a noisy process that accumulates relative information over time from a starting point to one of two decision boundaries. Once evidence has passed the boundary threshold, a decision has been made and the appropriate motor response is planned accordingly. Since the evidence gathered in aiding the decision is noisy, the process is stochastic and the state of the system is determined probabilistically. The probabilistic nature of this process has led to the recent proposal of a Bayesian approach to the DDM, the hierarchical drift diffusion model (HDDM; Wiecki et al. 2013). Parameters of the HDDM allow simultaneous estimation of subject and group parameters whereby individual subjects are assumed to be drawn from a group distribution. It is therefore possible to use HDDM to infer further information about eye movements under different conditions at the group level, above and beyond standard frequentist analyses of the data.

The speed at which the evidence accumulation process approaches one of two boundaries (e.g., choosing a red or blue item) is called the drift rate (v) and denotes the relative evidence for or against a particular response. The drift rate is a function of the value difference between two items, so a relatively high drift rate indicates an easy decision, with a lower drift rate indicating a more difficult decision. In the current experiment, each trial required a quick eye movement toward the target. Given that the angle and reward value of the distractor changed across trials, we expected to see differences in the drift rate, representing the disturbing influence of the distractor on the control of saccades to the target. A second important parameter in the HDDM is the separation between the two boundaries (a). If the boundaries are close together, then a noisy accumulation process reaches one of the boundaries quickly, but it is highly likely that some errors are made (a liberal decision). If the boundary separation is large, it indicates the need for greater evidence accumulation before a decision can be made, but once a decision has been reached it tends to be more accurate (a cautious decision). Since the current experiment required quick eye movements, with no changes in instruction or stimulus luminance across trials, we hypothesized that the boundary separation would remain constant throughout the task and that the boundaries would be close together, resulting in a risk of errors. To perform HDDM on our data, we used the open source HDDM Python toolbox created by Wiecki et al. (2013). Regarding other parameters of the model, we allowed variation in the starting point z of the decision process (z lies in range $[0,1]$; $z = 0.5$ suggests no a priori bias in the starting point). Non-decision time T_{er} is the combined time for stimulus encoding (before the decision process begins) and response execution once the decision has been made. We

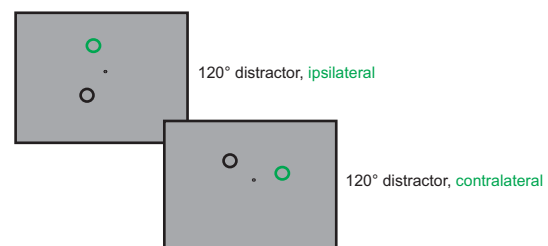


Fig. 3. Hemifield display for equidistant ipsilateral and contralateral distractor trials.

kept T_{er} fixed primarily for practical reasons, since allowing too many parameters in the model to vary can lead to unnecessary complexity in the design. We assumed any between- or within-individual variation in T_{er} to be of a lesser magnitude and importance than differences in other model parameters across our experimental conditions. The behavioral data provided to the full model comprised all correct and error trials from all participants and included response times (ms), response outcome (correct to target or incorrect to distractor), relative angle of the distractor (30°, 120°, or 180°), and reward value indicated by the distractor (high, low, or no reward). As with the frequentist data, trials in which the first saccade was anticipatory or late, contained blinks, or did not end at the target or distractor location were not included in the analysis. An additional hemifield model was also run in which only the 120° distractor trials were taken and labeled as either ipsilateral or contralateral to the target. Again, response times, response outcome, and reward value were taken for each trial, as in the full model, but with hemifield used instead of angle for the hemifield model. For each model, 10,000 samples were drawn; the first 1,000 were discarded ("burn in"), and every fifth sample from the remaining samples was taken and used to estimate the model parameters. These figures were chosen to ensure convergence of the model, which uses Markov chain Monte Carlo (MCMC) sampling techniques. Since the chains can be erratic at the beginning, the large number of discarded burn-in samples means this noisy initial period does not influence the final parameter estimation.

RESULTS

Exclusions

Because of inaccurate drift correction, 1 block of 90 trials was removed for 7 participants, and 2 blocks were removed for 2 participants. All 1,800 experimental trials were analyzed for the remaining 15 participants. Of these data, 78.51% (SD 6.63%) of first saccades were made to the target, 9.47% (SD 4.29%) were erroneous saccades to the distractor, and the remaining 12.02% (SD 5.96%) were saccades to a location that was considered neither target nor distractor. Of these trials, 0.75% (SD 1.13%) were discarded due to blinking during the saccade. Also, 1.60% (SD 1.05%) of trials were removed due to saccade onset latencies of less than 80 ms, and 6.03% (SD 2.35%) were discarded due to saccade arrival latencies greater than the participant's individual timeout (322 ± 40 ms).

Saccadic Latency

The mean saccadic latency of saccades across all participants and conditions was 166 ± 19 ms. A repeated-measures ANOVA was carried out on saccade latency of correct saccades to the target, with distractor angle (30°, 120°, or 180°) and reward type (high, low, or no) as factors (Fig. 4). This revealed a highly reliable main effect of angle [$F(2,46) = 92.72$, $P < 0.001$, $\eta_p^2 = 0.80$]. Saccades were initiated much faster to the target when a distractor was located at 30° than at either 120° [162.53 ± 3.45 vs. 178.47 ± 3.66 ms, respectively; $t(23) = 10.35$, $P < 0.001$] or 180° [180.45 ± 4.05 ms; $t(23) = 9.59$, $P < 0.001$]. Saccade latencies were also quicker when the distractor was at 120° than at 180° [$t(23) = 3.20$, $P = 0.004$]. There was no main effect of reward on latencies, nor any interaction between angle and reward ($P > 0.1$). However, planned paired-samples t -tests on the 180° distractor condition revealed a reliable difference in saccadic latency between high- and low-reward distractors, with slower saccadic latencies to the target when a high-reward distractor appeared at the mirror



Fig. 4. Saccade latency to the target. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

opposite location (180°) compared with a low-reward distractor at that location [181.60 ± 4.12 vs. 179.54 ± 3.99 ms; $t(23) = 3.45$, $P = 0.002$]. There were no significant differences between high- and no-reward or low- and no-reward distractor trials ($P > 0.1$). A two-tailed paired-samples t -test on saccade latencies to the target vs. saccades to the distractor, regardless of angle or reward condition, revealed that saccadic latencies to the distractor were considerably faster [158.92 ± 3.34 vs. 173.815 ± 3.56 ms, respectively; $t(23) = 8.527$, $P < 0.001$].

Saccadic Amplitude

Saccade amplitude is a measure of the size of the saccade in visual degrees. Correct saccades landing directly at the center of the target were expected to have an amplitude of 4.5°, because this was the eccentricity of the starting point to target in every trial. Since it was necessary to begin and end a saccade in a small predefined target region of interest for the experiment to continue, measurements of amplitude were taken as the size of the saccade in correct trials, without adjustments for the actual start or end point. Amplitude analysis was carried out on the deviance from the center of the target, with a positive result indicating an overshoot and a negative result indicating an undershoot to the target center. A repeated-measures ANOVA on saccade amplitude deviance with angle (30°, 120°, or 180°) and reward type (high, low, or no reward) as factors showed a main effect of angle [$F(2,46) = 8.87$, $P = 0.001$, $\eta_p^2 = 0.28$; see Fig. 5]. The deviance of the target saccade was more negative when a distractor was located at 30° from the target than at either 120° [$-0.17^\circ \pm 0.06^\circ$ vs. $-0.10 \pm 0.06^\circ$, respectively; $t(23) = 2.65$, $P = 0.01$] or 180° [$-0.08 \pm 0.06^\circ$; $t(23) = 3.35$, $P = 0.003$]. Furthermore, saccadic amplitude to the target was significantly shorter when the distractor was at 120° compared with 180° [$t(23) = 2.15$, $P = 0.04$]. The ANOVA also revealed a main effect of reward on saccade amplitude deviance [$F(2,46) = 5.86$, $P = 0.005$, $\eta_p^2 = 0.20$]. At each distractor angle, the high-reward distractor resulted in greater undershoot than both a low-reward distractor [$-0.15 \pm 0.06^\circ$ vs. $-0.10 \pm 0.06^\circ$, respectively; $t(23) = 2.85$, $P = 0.009$] and a no-reward distractor [$-0.10 \pm 0.06^\circ$; $t(23) = 3.02$, $P = 0.006$]. There was no difference in amplitude between low- and no-reward distractor trials ($P > 0.1$). Overall, eye movements fell slightly short of the target center on average, irrespective of distractor reward or angle.

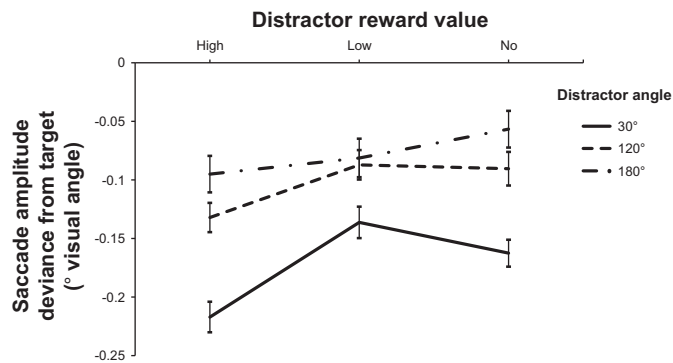


Fig. 5. Saccade amplitude deviance from the target. Negative deviance indicates an undershoot in the saccade. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

Erroneous Saccades

Of all allowed trials, 10.11% (SD 4.57%) (excluding blinks, anticipatory and slow responses) were erroneous saccades to the distractor circle. The percentage of the total erroneous saccades made per participant was taken for each distractor angle and reward combination. The higher the reward association of the distractor and the closer it was to the target, the more it erroneously captured the eyes, as revealed by a repeated-measures ANOVA (Fig. 6). The ANOVA showed both a main effect of distractor angle [$F(2,46) = 13.20$, $P < 0.001$, $\eta_p^2 = 0.37$] and a main effect of reward level [$F(2,46) = 6.16$, $P = 0.004$, $\eta_p^2 = 0.21$]. A distractor at 30° resulted in more erroneous saccades than a distractor at either 120° [$14.88 \pm 1.04\%$ vs. $10.45 \pm 0.50\%$; $t(23) = 3.03$, $P = 0.006$] or 180° [$8.00 \pm 0.72\%$; $t(23) = 4.00$, $P = 0.001$]. The 120° distractor also led to more errors than the 180° [$t(23) = 3.70$, $P = 0.001$]. High-reward distractors captured the eyes significantly more than distractors associated with no reward [$14.33 \pm 1.15\%$ vs. $8.38 \pm 0.77\%$; $t(23) = 3.57$, $P = 0.002$], with a trend for high-compared with low-reward distractors [$14.33 \pm 1.15\%$ vs. $10.62 \pm 1.02\%$; $t(23) = 1.83$, $P = 0.08$]. There was no reliable difference in erroneous saccades to the low- over no-reward distractor ($P > 0.1$).

Distribution of Erroneous Saccades Across Latencies

Percentages of erroneous saccades to the distractor were calculated for the latency quartiles of each individual participant's unique latency distribution per reward condition (Fig.



Fig. 6. Percentage erroneous saccades to distractor. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

7), as described in MATERIALS AND METHODS. A 3×4 repeated-measures ANOVA with reward (high, low, or no) and latency bin (fastest to slowest quartiles) revealed a main effect of reward regardless of latency bin [$F(2,46) = 6.15$, $P = 0.004$, $\eta_p^2 = 0.21$], with the high-reward distractor leading to significantly more erroneous saccades than the no-reward distractor across all bins [$t(23) = 3.57$, $P = 0.002$] and a trend for high-over low-reward distractors [$t(23) = 1.83$, $P = 0.08$]. A main effect of latency bin was found and expected, given that the data were first split into quartiles [$F(3,69) = 9.20$, $P < 0.001$, $\eta_p^2 = 0.29$]. There was no reward \times latency bin interaction; the shape of each reward level data was similar across bins, suggestive of a simple additive effect of reward on the distribution of the data, especially for high and low reward. It is important to note that even the mean latency of the slowest saccade quartile was still considerably fast (186.45 ± 4.61 ms, for the high-reward condition), which could explain the relatively stable effect of reward across time bins, with no interaction later in time.

Global Effect

The global effect is usually observed when two stimuli are in close proximity, specifically when the polar angle between them is $\leq 30^\circ$. Thus correct 30° distractor trials were analyzed for differences in landing position (see MATERIALS AND METHODS for approach). For each participant these were split into either fast or slow saccades, according to the median saccadic onset latency for that participant across all correct 30° distractor trials. A positive percentage indicates a landing position closer to the target-distractor midpoint, thereby indicating a landing position closer to the distractor. A repeated-measures ANOVA was performed on these data, with latency (fast or slow) and reward (high, low, or no) as factors (Fig. 8). This revealed a main effect of latency [$F(1,23) = 19.90$, $P < 0.001$, $\eta_p^2 = 0.46$], as well as a main effect of reward [$F(2,46) = 6.78$, $P = 0.003$, $\eta_p^2 = 0.23$], with no interaction between the two. Eye movements were closer to the target-distractor midpoint (thus closer to the distractor) when a high-reward distractor was presented compared with both a low-reward [$5.44 \pm 2.37\%$ vs. $-0.65 \pm 3.10\%$; $t(23) = 3.05$, $P = 0.006$] and no-reward distractor [$-0.487\% \pm 2.36\%$; $t(23) = 4.21$, $P < 0.001$], regardless of latency. There was no difference in target landing position between low- and no-reward distractor saccades ($P > 0.1$). Faster saccades resulted in a landing location closer to the distractor

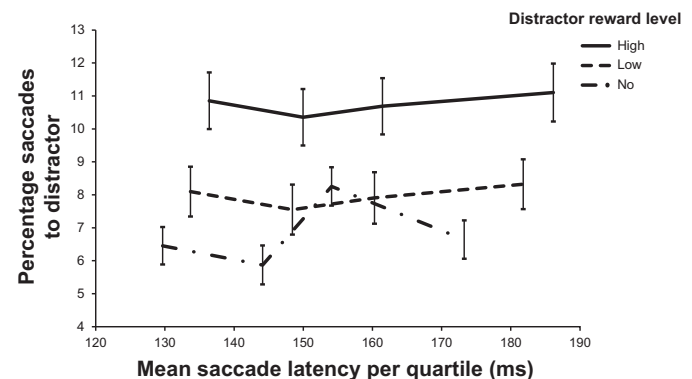


Fig. 7. Percentage saccades to distractor per quartile latency bin. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

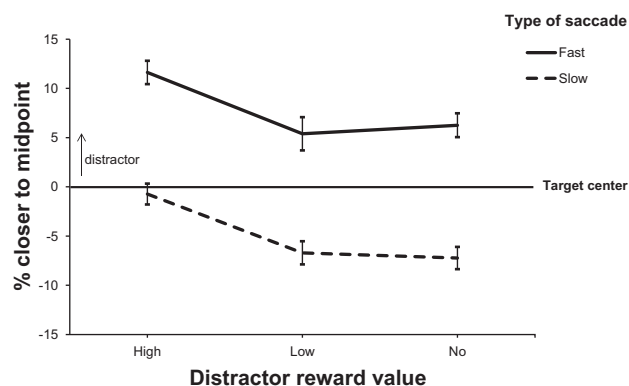


Fig. 8. Percentage closer to target-distractor midpoint for fast and slow saccades. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

$[7.76 \pm 3.31\%$ vs. $-4.89 \pm 2.13\%$; $t(23) = 4.461$, $P < 0.001$], irrespective of reward level.

Saccadic Curvature

As described in MATERIALS AND METHODS, we employed the peak deviance approach to analyze curvature of correct saccades to the target. Curvature was calculated for the 30° and 120° distractor trials only, because it was not possible to define curvature as being either toward or away from the 180° distractor. A repeated-measures ANOVA with angle and reward level showed a significant main effect of angle [$F(2,46) = 29.98$, $P < 0.001$, $\eta_p^2 = 0.556$; see Fig. 9]. The smallest distractor angle of 30° led to less curvature toward the distractor than 120° , irrespective of reward value [0.03 ± 0.01 vs. 0.05 ± 0.01 ; $t(23) = 5.48$, $P < 0.001$]. There was also a significant interaction between reward and angle [$F(4,92) = 3.70$, $P = 0.03$, $\eta_p^2 = 0.14$], influenced mainly by the low-reward distractor at 120° resulting in greater curvature than the high- and no-reward distractors. This effect is described in more detail below, where we investigate the effects of visual hemifield on oculomotor capture.

Learning

Given that participants were not explicitly informed of the distractor color-reward contingency, we expected this to be learned as the experiment progressed. For learning analyses the experiment was divided into five main blocks (each containing



Fig. 9. Curvature of saccades toward distractor for correct saccades to target. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

4 mini-blocks, to make up the complete 20 mini-blocks of the experiment). Whether participants learned the association between color and reward magnitude was expected to be reflected in the number of erroneous saccades to the distractor; if an association is learned, one expects the eyes to be captured more by a high-value distractor relative to a distractor with lower value. To that end, we performed a repeated-measures ANOVA on the percentage of erroneous saccades with distractor angle (30° , 120° , or 180°), reward value (high, low, or no reward), and block (1–5) as factors. This revealed a main effect of reward [$F(2,46) = 6.15$, $P = 0.004$, $\eta_p^2 = 0.21$] and, crucially, a reward \times block interaction [$F(8,184) = 2.60$, $P = 0.01$, $\eta_p^2 = 0.10$; see Fig. 10]. A main effect of angle [$F(2,46) = 13.00$, $P < 0.001$, $\eta_p^2 = 0.36$] and an interaction between angle and block [$F(8,184) = 2.11$, $P = 0.037$, $\eta_p^2 = 0.08$] was also visible in erroneous saccades. Two-tailed paired-samples t -tests on reward value for individual blocks, regardless of angle, revealed no significant differences in reward level in the first two blocks, with substantial differences emerging in the third block, particularly between high and no reward [$3.03 \pm 0.36\%$ vs. $1.89 \pm 0.25\%$; $t(23) = 2.35$, $P = 0.028$]. This difference in erroneous saccades toward high- over no-reward-signaling distractors remained reliable for the rest of the experiment [$2.80 \pm 0.26\%$ vs. $1.27 \pm 0.16\%$; $t(23) = 3.98$, $P = 0.001$ and $3.54 \pm 0.51\%$ vs. $1.40 \pm 0.21\%$; $t(23) = 3.70$, $P = 0.001$ for blocks 4 and 5, respectively]. These results clearly indicate that participants learned the association between distractor color and reward magnitude, causing them to progressively make more erroneous saccades to distractors signaling high-magnitude reward.

Summary of Effects

The results presented above reveal faster saccade latencies for the smallest distractor angle (30°) compared with larger angles (120° and 180°). Distractor reward level only appeared to play a small role at the greatest distractor angle (180°), indicating a slowing down in saccade latency to the target when a high- compared with low-reward distractor was present. The greatest undershoot in saccade amplitude was seen for the 30° distractor. At each distractor angle, the high-reward distractor led to greater undershoot of the target than low- and no-reward distractors. The greatest oculomotor capture (in-

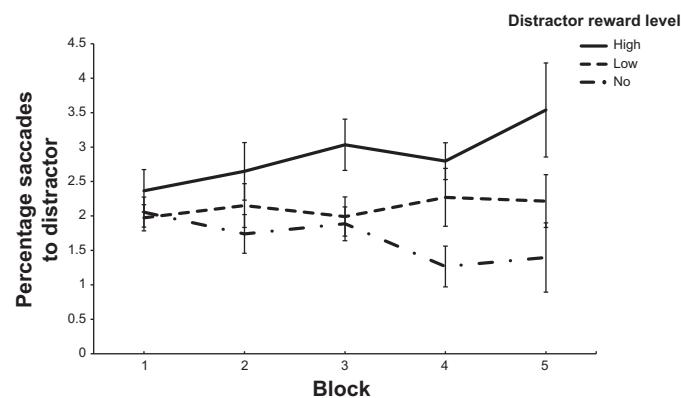


Fig. 10. Learning of the distractor color-reward association, represented as the percentage of erroneous saccades to the distractor across blocks. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

dexed by erroneous saccades) was also seen for the 30° distractor, followed by the 120° and 180° distractor, respectively. There was greatest reward capture by the high-reward distractor, at each distractor angle. This effect was robust across all latency quartiles, although all saccades in the task were considerably fast. The global effect was observed, with the eyes landing closer to the distractor for the fastest half of saccades. The landing position was also closest to the distractor when a high-reward distractor was present compared with low- and no-reward distractors, regardless of saccade latency. Saccadic curvature was greater for the larger compared with smaller distractor angle (120° vs. 30°), with distractor reward value having no differentiating effect on this property. The learning of the distractor color-reward association was reflected in the percentage of erroneous saccades made to the distractor throughout the course of the experiment; participants increasingly made more erroneous saccades toward the high- than the no-reward-signaling distractor as the experiment progressed.

Visual Hemifield

Although the physical distance between the target and distractor was the same, the relative hemifield of the 120° distractor led to differences in saccadic latency of correct saccades, percentage of erroneous saccades to the distractor, and saccadic curvature. Total percentages of ipsilateral and contralateral hemifield trials were similar (16.27% vs. 16.08% of all experimental trials, $P > 0.1$).

Saccadic latency. When a 120° distractor was presented in the contralateral hemifield to the target, there was a significant increase in saccadic latencies toward the target, compared with ipsilateral hemifield presentation. A repeated-measures ANOVA with hemifield (ipsilateral or contralateral) and reward levels (high, low, no) as factors demonstrated this main effect of hemifield on saccadic latency [$F(1,23) = 20.783$, $P < 0.001$, $\eta_p^2 = 0.475$; see Fig. 11]. Saccadic latencies for the different reward levels were affected in a similar way across hemifield ($P > 0.1$). A two-tailed paired-samples t -test on saccade latency of erroneous saccades to the distractor when the distractor was in the ipsilateral vs. contralateral hemifield, regardless of angle or reward condition, showed that saccadic latencies to the distractor were considerably faster when the distractor was in the contralateral hemifield [158.19 ± 3.23 vs.

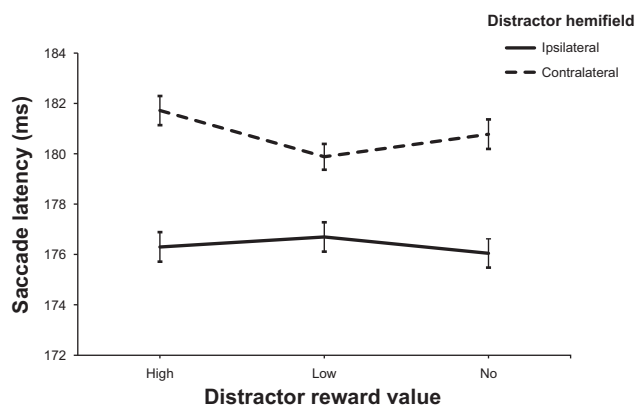


Fig. 11. Saccade latency to target for ipsilateral and contralateral distractor hemifield. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

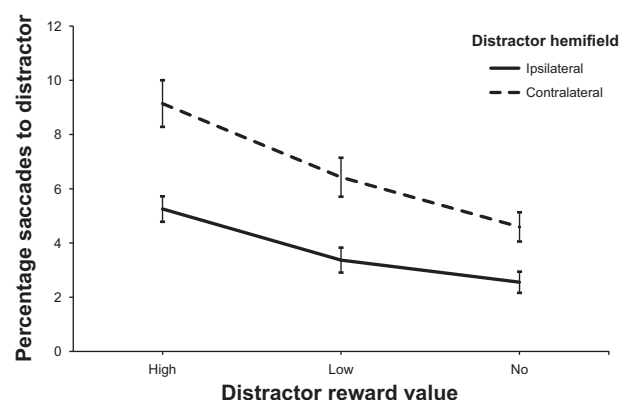


Fig. 12. Percentage of saccades to distractor for ipsilateral and contralateral distractor hemifield. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

170.50 ± 4.52 ms for contralateral vs. ipsilateral distractors; $t(23) = 4.321$, $P < 0.001$].

Erroneous saccades. A repeated-measures ANOVA on erroneous saccades with hemifield and reward level as factors revealed a similar pattern of erroneous saccades as shown in Fig. 6 (see Fig. 12). Distractors presented at 120° showed a main effect of reward level on the proportion of saccades made to the distractor, when the distractor was presented both ipsilateral and contralateral to the target [$F(2,46) = 8.67$, $P = 0.001$, $\eta_p^2 = 0.27$]. Furthermore, distractors in the contralateral hemifield resulted in a significantly greater proportion of saccades toward them than distractors presented in the ipsilateral hemifield [$F(1,23) = 23.79$, $P < 0.001$, $\eta_p^2 = 0.51$].

Saccadic curvature. A repeated-measures ANOVA on curvature with hemifield and reward level as factors showed that although the physical distance was the same, trials in which a distractor was presented in the ipsilateral hemifield to the target led to considerably more curvature than trials with a distractor appearing in the contralateral hemifield [$F(1,23) = 6.34$, $P = 0.02$, $\eta_p^2 = 0.22$], as shown in Fig. 13. This effect was present for all reward levels.

Summary of visual hemifield effects. Distractors presented remote from a target (at 120°) but in the contralateral hemifield resulted in slower saccades to the target, with more erroneous saccades toward the distractor than when distractors were presented at the same physical distance from the target but in the ipsilateral hemifield. Ipsilateral presentation of distractors

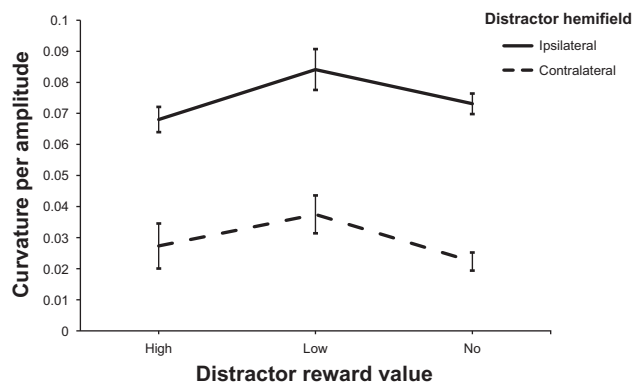


Fig. 13. Curvature of target saccades toward distractor for ipsilateral and contralateral distractor hemifield. Error bars show \pm SE normalized for within-subject design (Cousineau 2005; Loftus and Masson 1994).

instead led to greater curvature toward the distractor than contralateral distractors. These findings (more capture and slower saccades) suggest that a remote distractor in the contralateral hemifield has a much larger effect on oculomotor behavior than a distractor presented at the same distance within the same hemifield. Once the saccade is initiated, there seems to be more competition from the ipsilateral relative to the contralateral distractor as evidenced by the larger curvature for ipsilateral distractors. Note that the effect on latency and curvature does not depend on reward value, whereas the amount of capture does.

Bayesian Hierarchical Drift Diffusion Modeling

Parameters for the HDDM models were estimated according to the details in MATERIALS AND METHODS. In a similar approach to the frequentist analyses, one model was based on all data ("full model"), and another was based on data collected only for the 120° distractor angle condition, to assess the effect of hemifield ("hemifield model").

General parameters. Tables 1 and 2 show the results for all parameters of each model (see MATERIALS AND METHODS for description), including boundary separation (a), nondecision time (T_{er}), starting point bias (z), and drift rates (v). Because of decisions made regarding the noise parameter in the creation of the HDDM package, the a , z , and v parameters must be multiplied by 0.1 when comparisons are made to standard DDM estimates in the literature (e.g., Ratcliff and Rouder 1998). Similarly, it is also necessary to multiply the z parameter by a to get the a comparable starting bias. As expected, the boundary separation a (0.91 and 0.77 for the full and hemifield model, respectively) was smaller than in other tasks analyzed with a DDM (e.g., Ratcliff et al. 1999), since the current task was a relatively easy, fast-paced eye movement paradigm. The starting point z ($z \times a = 0.23$ and 0.22 for the full and hemifield model, respectively) indicated a bias closer to the error boundary, meaning errors were fast compared with correct responses. This is in line with the frequentist results comparing saccade latencies of correct and errors trials. The Bayesian full model estimate of non-decision time T_{er} suggests that ~90 ms were spent on combined stimulus encoding and motor response planning for the full model (Table 1).

Table 1. Full model parameters of the HDDM

Model Parameters	Mean
a	0.912
z	0.250
T_{er}	90
v (30.high)	7.593
v (30.low)	7.828
v (30.no)	7.910
v (120.high)	6.237
v (120.low)	6.729
v (120.no)	6.940
v (180.high)	6.191
v (180.low)	6.781
v (180.no)	6.956

The boundary separation (a), starting point bias (z), and drift rate values (v) may be multiplied by 0.1 to make parameters comparable to standard drift diffusion model estimates in the literature (e.g., Ratcliff and Rouder 1998). The factor of 10 is due to the choice of a scaling parameter used by the hierarchical drift diffusion model (HDDM). Legend also applies to Table 2.

Table 2. Hemifield model parameters of the HDDM

Model Parameters	Mean
a	0.766
z	0.291
T_{er}	108
v (same.high)	6.980
v (same.low)	7.454
v (same.no)	7.533
v (opp.high)	5.832
v (opp.low)	6.525
v (opp.no)	6.843

Drift rate. Posterior probability distributions of drift rate were estimated for each distractor angle and reward combination of the full model (Fig. 14) and for each hemifield and reward combination of the hemifield model (Fig. 15). Hypothesis testing was done directly on the posteriors of the conditions, assessing the probability that one posterior distribution is statistically different from another. Tables 3–6 show these probabilities for comparisons between full model distractor angles and reward levels (Tables 3 and 4) and between hemifield model distractor hemifield and reward levels (Tables 5 and 6). The term $P(X < Y)$ gives the probability that the posterior distribution of the drift rate for *condition X* is less than that of *condition Y*. Comparison between angles in the full model largely reflects earlier analyses on saccadic latencies; there is a high certainty that the drift rate for larger angles (180° and 120°) is statistically lower than that for a smaller angle (30°) at each reward level, meaning that quicker decisions were made in the small-angle condition (Fig. 14 and Table 3). The greatest differences between reward levels were seen particularly in the 180° case [Fig. 14 and Table 4; $P(\text{high} < \text{no}) = 0.875$, $P(\text{high} < \text{low}) = 0.816$], which was also highlighted in the results on saccadic latency using frequentist analysis. However, the HDDM model additionally indicated differences in reward at smaller angles, with $P(\text{high} < \text{no}) = 0.860$ and $P(\text{high} < \text{low}) = 0.781$ for the 120° condition, and $P(\text{high} < \text{no}) = 0.687$ for the 30° condition. The results suggest slower drift rates (slower decision latencies) in those trials where the high-reward distractor was

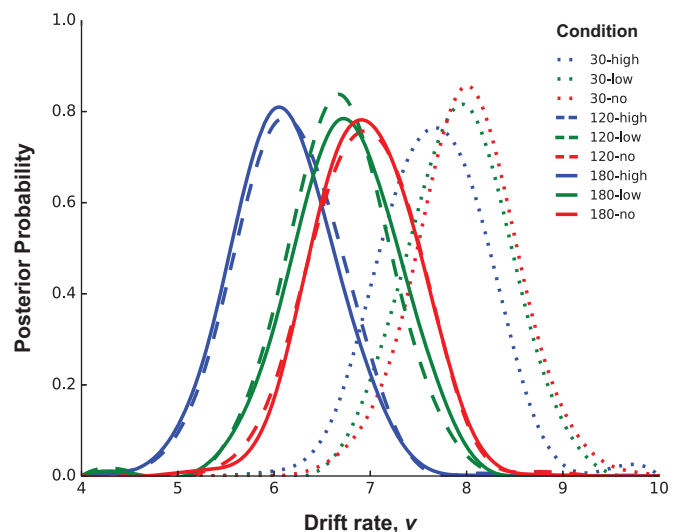


Fig. 14. Full HDDM model showing posterior distributions for drift rate v per distractor angle (30°, 120°, or 180°) and reward condition (high, low, or no).

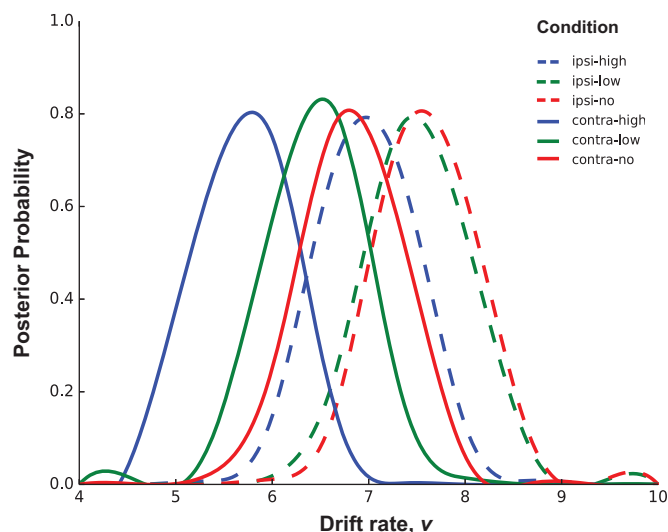


Fig. 15. Hemifield HDDM model showing posterior distributions for drift rates v per distractor hemifield (ipsilateral or contralateral to target) and reward condition (high, low, or no).

present, compared with both low- and no-reward trials, in every distractor angle condition.

The hemifield model clearly shows slower drift rates when distractors were presented in the contralateral compared with ipsilateral hemifield [Fig. 15 and Table 5; $P(\text{contra} < \text{ipsi}) = 0.974, 0.931, \text{ and } 0.866$ for high-, low-, and no-reward distractors, respectively]. This consolidates the saccadic latency results for hemifield found earlier. However, as with the HDDM full model, the hemifield model similarly estimated substantial differences in drift rate for the different reward levels that were not seen in the frequentist analysis (Table 6). When distractors were presented at 120° in either hemifield, the drift rate was lower when the distractor was highly re-

Table 3. Probabilities that drift rates are different across conditions for the full model: angle comparison

Reward	Angle	Probability ($X < Y$)
High	X: 180°	0.984
	Y: 30°	
	X: 180°	0.532
	Y: 120°	
	X: 120°	0.977
Low	X: 180°	0.944
	Y: 30°	
	X: 180°	0.459
	Y: 120°	
	X: 120°	0.960
No	X: 180°	0.924
	Y: 30°	
	X: 180°	0.489
	Y: 120°	
	X: 120°	0.928
	Y: 30°	

Probability ($X < Y$) gives the probability that the posterior distribution of the drift rate for condition X is less than that of condition Y . A value of 0.5 indicates largely overlapping traces. The closer the result is to 1, the more certain that X and Y are statistically different (condition X is slower to reach the boundary than condition Y). Legend also applies to Tables 4–6.

Table 4. Probabilities that drift rates are different across conditions for the full model: reward comparison

Angle	Reward	Probability ($X < Y$)
30°	X: high	0.687
	Y: no	
	X: high	0.650
	Y: low	
	X: low	0.548
120°	X: high	0.860
	Y: no	
	X: high	0.781
	Y: low	
	X: low	0.626
180°	X: high	0.875
	Y: no	
	X: high	0.816
	Y: low	
	X: low	0.614
	Y: no	

warded, especially compared with no-reward distractor trials. This reward effect was stronger when the distractor was presented in the contralateral hemifield [$P(\text{high} < \text{no}) = 0.951$ and 0.824 for contralateral and ipsilateral hemifield, respectively].

Results from both HDDM models therefore indicate greater competition from high-reward distractors at larger angles to the target, specifically those presented in the contralateral hemifield, resulting in longer deliberation time before an eye movement is made.

Model comparison and quality. Because a number of models could explain the observed data, we sampled four separate models and compared the deviance information criterion (DIC) obtained for each. DIC is a hierarchical modeling generalization of the AIC (Akaike information criterion) and BIC (Bayesian information criterion). Since we provide the HDDM with information regarding different experimental conditions (e.g., distractor angle and reward level), we can choose which explanatory variables to include in the model. Important model parameters such as drift rate and boundary separation can also vary or remain fixed. Thus testing numerous models with differing combinations of these variables and parameter limitations allows us to compare and assess which model best fits the data. DIC results in Table 7 confirm that the model that allowed a varying drift rate according to angle and reward condition (our “full model”) explained the data best, as indicated by the lowest DIC. The additional model allowing for

Table 5. Probabilities that drift rates are different across conditions for the hemifield model: hemifield comparison

Reward	Hemifield	Probability ($X < Y$)
High	X: contralateral	0.974
	Y: ipsilateral	
Low	X: contralateral	0.931
	Y: ipsilateral	
No	X: contralateral	0.866
	Y: ipsilateral	

Table 6. Probabilities that drift rates are different across conditions for the hemifield model: reward comparison

Hemifield	Reward	Probability ($X < Y$)
Ipsilateral	X: high	0.824
	Y: no	
	X: high	0.781
	Y: low	
	X: low	0.569
Contralateral	Y: no	
	X: high	0.951
	Y: no	
	X: high	0.870
	Y: low	
	X: low	0.700
	Y: no	

changes in the boundary separation as well as the drift rate was worse at explaining the data than any of the other drift rate only models.

Model convergence. The R-hat Gelman-Rubin statistic was used to assess chain convergence of the model (Gelman and Ruben 1992). This involved running multiple chains and checking whether they all converged to the same stationary distribution. The statistic then compared between-chain variance to within-chain variance. R-hat values for the three parameters a , T_{cr} , and v were 1.000, 1.001, and 1.000, respectively. These values were all below 1.1, indicating successful convergence of all chains. Visual inspection of the trace plots for parameters a , T_{cr} , z , and all v suggested good mixing of the chains, which moved easily around the parameter space.

Quality of model fit. Posterior predictive checks may be used to assess whether the model can reproduce important patterns in the data. New data were simulated from the posterior of the fitted model, and statistics on these data were compared with the model data to see that a key pattern has been replicated. Using the *post_pred_gen()* function from the HDDM toolbox, a different data set for 500 parameter values was simulated from the posterior of the fitted model. Numerous summary statistics were then compared (including accuracy, mean of upper/lower boundaries, standard deviation of upper/lower boundaries, and quantiles) and deemed reliable if the comparison fell within the 95% credible interval. All summary statistics comparisons between the respective fitted full or hemifield model and simulated full or hemifield model were credible.

DISCUSSION

We systematically examined the effect of reward-signaling distractors on oculomotor control in a novel, continuous, fast-paced eye movement task. The results show that classic properties of oculomotor behavior such as the global effect and the remote distractor effect are affected by distractor reward value. Increased erroneous saccades to the distractor (i.e., oculomotor capture) occur for distractors of increasing value, even though making these erroneous saccades was detrimental to reward pay-out (see also Failing et al. 2015; Le Pelley et al. 2015 for a similar effect). Even though moving the eyes to the distractor resulted in the omission of reward, observers could not seem to prevent it, providing strong evidence that the reward-signaling distractor captured the eyes against the top-down intentions of the observer. This finding is in line with the theory of Awh et

al. (2012) describing the additional component of reward history effects on visual responses, above and beyond the standard theories of endogenous and exogenous influences. Bayesian hierarchical drift diffusion modeling, informed by both individual and group parameters, was used to highlight differences in saccade latency distributions and errors in oculomotor control, depending on the reward value associated with a distractor in the environment. Taken together, these findings suggest that even in the very simplest contexts of stimulus processing, reward opportunities and the relative location of reward-signaling distractors play an important role in oculomotor control.

Classic Eye Movement Effects

We replicated several classical eye movement effects with distractors that signal reward. First, we demonstrated that the remote distractor effect (Walker et al. 1997) is sensitive to reward value; a high-reward-signaling distractor presented at the opposite side of the target (at 180°) had a larger effect on saccade latency than a low-reward-signaling distractor. Second, we showed that the global effect was modulated by reward value. For distractors presented close to the target (at 30°), we saw that the saccade amplitude (Fig. 5) and saccade landing position (Fig. 8) were strongly modulated by reward value with shorter saccade latencies, landing closer to the distractor for high vs. low reward value. Reward value did not modulate saccade latencies for 30° distractors (see Fig. 4). Third, reward value had a large effect on errors in oculomotor control; more saccades were made to the distractors when they signaled high reward value than when they signaled low or no reward value (Fig. 6). We also show a larger increase in errors across blocks for high-reward-signaling distractors (Fig. 10), demonstrating a learning effect as participants gradually made the distractor color-reward association, despite its detrimental effect on total reward payment. Previous studies in which participants were explicitly informed of the distractor color-reward relationship showed a relatively stable difference between erroneous saccades to high- compared with low-reward-signaling distractors across the whole experiment (Failing et al. 2015; Le Pelley et al. 2015). The current study demonstrates that people can learn this stable association for themselves. Since the distractor color was never mentioned and looking to the distractor was counterproductive to succeeding in the task, this approach eliminated a top-down, instruction-based explanation for these erroneous saccades.

Saccade Amplitude and Landing Position

Distractors signaling reward affected saccade amplitude and landing position (cf., the global effect). The undershoot in

Table 7. DIC results for 4 models

Model	DIC
v : angle only	−126723.253
v : reward only	−126340.070
v : angle and reward	−127307.558
v : angle and reward	
a : angle and reward	−120430.048

Values are deviance information criterion (DIC) for 4 models. v means the drift rate is allowed to change according to the indicated condition; a means the boundary separation may change.

amplitude to the target center observed when a distractor was present was amplified by a high-reward distractor at each location. Few studies have looked into the effects of reward on saccadic amplitude. Those studies that have assessed amplitude investigated it in relation to rewarded or nonrewarded eye movement directions (Shimo and Hikosaka 2001; Takikawa et al. 2002), reporting a decrease in the variation of amplitude for the rewarded direction but with no significant changes in mean amplitude between these conditions. The current study shows that there are reward-related changes in the amplitudes of target-directed saccades in the presence of a reward-signaling distractor. A similar effect was also seen in the landing position of saccades to the target; distractors associated with high reward led to saccade endpoints closer to the distractor than low- or no-reward distractors. This was the case for both fast and (relatively) slower saccades, with fast saccades in the presence of high reward resulting in a landing position closer to the distractor than in any other condition. A previous study investigating the effect of reward value on saccades to two target circles placed in close proximity to each other revealed a shift in the center of gravity toward the more highly valued stimulus (Bucker et al. 2015). We found that the high reward value of a distractor also led to a shift in the landing position toward the distractor, even though in the current study (unlike that of Bucker et al.) a saccade to the distractor resulted in losing the reward for that trial.

Brain Mechanisms

As mentioned in the Introduction, neurons in LIP represent salience and object-value information, encoding the location of attention-worthy objects in the visual scene (Gottlieb et al. 2014). LIP output can be fed directly to the SC, but also to the CD in the BG. The CD acts as a gateway for gaze control, projecting to the SC via the SNr (inhibitory connections). Decreases in SNr spiking activity lead to the “release” of the SC, essentially disinhibiting it (Hikosaka and Wurtz 1983). It has been suggested that the head and body of the CD encode reward values flexibly, relying on short-term memory (Kawagoe et al. 1998; Sato and Hikosaka, 2002), whereas the CD tail (CDt) is responsible for long-term value memory, when objects are associated with low or high reward consistently and stably (Yamamoto et al. 2013). It was recently shown that increased CDt neuronal firing resulting from stably high-rewarded objects leads to the inhibition of SNr neurons, whereas reduced CDt firing from stably low-rewarded objects (in a relative setting) leads to excitation of the SNr, resulting in SC disinhibition or inhibition, respectively (Yasuda et al. 2012). Monkeys in this study gradually acquired a preference for making saccades to high-valued over low-valued objects quickly and automatically, even when a reward was not immediately delivered anymore. We believe distractor reward-signaling encoding in the current study operates via a similar mechanism whereby the CDt-SNr-SC circuit is trained inadvertently to acquire a preference for the high-value signaling color, despite its effect on reward payment.

Competitive Integration

Many oculomotor effects reported in this article are consistent with the competitive integration account of saccadic programming, as described by Godijn and Theeuwes (2002) (see

also Meeter et al. 2010; Mulckhuyse et al. 2009; Trappenberg et al. 2001). This model assumes that exogenous (e.g., sensory information) and endogenous (voluntary) inputs are integrated in the SC on a common saccade map. When a target and distractor are close together in the visual field, the combined activation on the SC saccade map converges to a local maximum somewhere between these two neighboring locations. However, if the target and distractor are far apart, there is mutual inhibition until attention is directed toward the target location, leading to lateral inhibition of the remote distractor below baseline activation. The competitive integration account establishes a time course for the activation of the SC saccade map (Godijn and Theeuwes 2002), suggesting that in the earliest phase there is activation at the salient distractor location, with corresponding deactivation at all other locations including the target. This is followed by a rise in activation of the target location so that both target and distractor locations are similarly active. In later stages, the target location becomes most active, passing a threshold for saccade execution to occur (for description of such a threshold in the FEF, see Hanes and Schall 1996; Heitz and Schall 2012), whereas the distractor (and fixation) locations fall below baseline for successful inhibition. The mechanisms by which endogenous signals are integrated with sensory information were investigated in a recent study of the monkey SC (Dorris et al. 2007), in a task in which the target location is fully predictable (an endogenous signal). A large early peak in neural activity was found in the SC for erroneous saccades to the distractor, whereas correct saccades to the target were represented by an early subthreshold peak and a larger suprathreshold peak later in time corresponding to the eye movement. Our finding demonstrating faster saccade latencies to the distractor than to the target is in line with this time course description. This behavior is also similar to results from anti-saccade tasks, in which participants refrain from making an eye movement to a target and instead make a saccade in the opposite direction (Munoz and Everling 2004), thereby relying on top-down inhibition of an automatic saccade to the target. Furthermore, the finding that fast saccades land closer to the distractor than slower saccades (Fig. 8) is consistent with the competitive integration model. Crucially, this effect is stronger for high-value relative to low-value distractors, indicating that the high-value distractor reaches threshold faster.

Visual hemifield effects. The effects of reward were strongly modulated by visual hemifield; relative to ipsilateral, distractors presented contralateral to the target caused more oculomotor capture (Fig. 12) and had a larger effect on saccade latencies, with slower saccades to the target for contralateral vs. ipsilateral distractors (Fig. 11). This suggests that the competition evoked by the distractor was larger when presented within the hemifield that did not overlap with the hemifield of the target. This result is consistent with the notion that there is more suppression of the distractor activation when a target and distractor are presented within the same hemifield (with more overlapping neural representation) than between hemifields. Indeed, when presented in the contralateral hemifield, the distractor activation may rise faster to threshold than within hemifield, since the mutual inhibition between hemifields is assumed to be much less than within hemifield (Hickey and Theeuwes 2011). This can be explained by the topography of a number of oculomotor-related brain regions, such as the

SC and SNr. These structures contain maps with spatial representation mainly for the contralateral visual hemifield (Hikosaka et al. 2000). Since objects in separate hemifields are encoded in separate populations of neurons, there is thus less mutual inhibition across hemifields than within hemifield. We also found that visual hemifield played a role in the remote distractor effect; in addition to demonstrating increased saccade latencies when a distractor was placed at the mirror-opposite location to a target (Levy-Schoen 1969; Walker et al. 1997), we showed that the remote distractor effect exists for increasing distance from the target (increased latencies for 180° compared with 120°), and also for distractors in the contralateral hemifield to the target compared with an equidistant distractor in the same hemifield. Visual hemifield effects on target processing have been investigated in several attentional tracking and visual search tasks (Alvarez and Cavanagh 2005; Luck et al. 1989). These studies concluded that hemifield independence is a signature of multifocal spatial selection, sometimes referred to as two separate “spotlights of attention,” one for each hemifield. The reduced capacity to track and process items within the same hemifield has been explained in terms of competition between neighboring locations. In line with competitive integration, in which there is greater competition between items presented in the same hemifield (e.g., Stoermer et al. 2014), we also show greater curvature for distractors presented at a remote location ipsilateral to the target compared with those presented equidistant in the contralateral hemifield. Overall, we demonstrate that a remote distractor in the contralateral hemifield has a large effect on saccade planning (slower latency, erroneous saccade endpoint) and that a remote distractor in the ipsilateral hemifield has a large effect on saccade execution (greater curvature). This has been explained in terms of the distinct or overlapping neural representation of space for each hemifield in oculomotor-related brain areas.

Hierarchical Drift Diffusion Modeling

Bayesian HDDM was used to analyze inter- and intra-individual differences and similarities in saccade latencies and errors. The hierarchical framework of HDDM allowed us to overcome some limitations associated with frequentist analysis, such as the assumption that all subjects are the same and are copies of an “average subject” (Wiecki et al. 2013). The HDDM instead uses both individual and group parameters to inform and constrain each other. This model revealed a much more robust effect of reward on saccadic latencies while also taking erroneous behavior into account in the estimation. Figure 14 shows that at each distractor angle, the high-reward distractor elicited a posterior probability distribution centered at the lowest drift rate (slowest latency) compared with low- and no-reward distractors. Like the frequentist results, this is most apparent at the largest distractor angle of 180°; however, HDDM also provides evidence for reward differences at smaller angles, particularly for high reward compared with low and no reward. This model further confirmed the large-effect results of distractor location found in the frequentist analysis, namely, a substantially higher drift rate (faster latencies) at smaller angles. The HDDM hemifield model presented in the current study emphasizes differences in eye movement latencies when reward-signaling distractors appeared ipsilateral or

contralateral to the target. The model clearly shows a slower drift rate (slower saccade latency) for contralateral distractors. Furthermore, the effect of reward value can be seen in both ipsilateral and contralateral domains, with high-reward distractors substantially slowing down the initiation of an eye movement. Results from this model suggest greatest capture of attention by remote, high-reward-signaling distractors appearing contralateral to a target. Since the HDDM drift rate is analogous not to only saccade latencies but also takes the distribution of errors into account, it may be seen as a complementary technique to standard frequentist analyses. The incorporation of saccade latencies and errors, within and across individuals, into a single framework makes HDDM a powerful tool in analyzing decision-making behavior, even for a fast, continuous eye movement task as presented in the current study.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

B.M. and J.T. conception and design of research; B.M. performed experiments; B.M. analyzed data; B.M. and J.T. interpreted results of experiments; B.M. prepared figures; B.M. and J.T. drafted manuscript; B.M. edited and revised manuscript.

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