Effects of reward on the accuracy and dynamics of smooth pursuit eye movements

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Abstract

Reward modulates behavioral choices and biases goal-oriented behavior, such as eye or hand movements, towards locations or stimuli associated with higher rewards. We investigated reward effects on the accuracy and timing of smooth pursuit eye movements in four experiments. Eye movements were recorded in participants tracking a moving visual target on a computer monitor. Prior to target motion onset, a monetary reward cue indicated whether participants could earn money by tracking accurately, or whether the trial was unrewarded (experiments 1-2; n=11 each). Reward significantly improved eye-movement accuracy across different levels of task difficulty. Improvements were seen even in the earliest phase of the eye movement, within 70 ms of tracking onset, indicating that reward impacts visual-motor processing at an early level. We obtained similar findings when reward was not precued but explicitly associated with the pursuit target (experiment 3, n=16); critically, these results were not driven by stimulus prevalence or other factors such as preparation or motivation. Numerical cues (experiment 4, n=9) were not effective.

Keywords: reward, expected value, eye movements, smooth pursuit, motivation, prevalence

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When we view our dynamic visual environment, our eyes are constantly in motion. We move our eyes in order to see better, to align gaze with an object of interest, allowing high-acuity visual perception of spatial and temporal target features (Kowler, 2011; Land, 1999). Smooth pursuit eye movements are continuous, slow eye movements that help us center and stabilize the image of a moving visual object on the retina, critical for activities requiring dynamic high-acuity vision (Lisberger, 2010; Spering & Montagnini, 2011). Whereas accurate smooth pursuit matters when predicting visual motion (Spering, Schütz, Braun & Gegenfurtner, 2011) –when a hitter judges the speed and angle of a baseball or a driver estimates the speed of an approaching vehicle– most smooth pursuit laboratory tasks simply require tracking without feedback or consequences. The present study investigates effects of expected reward, manipulated via assigning a monetary reward to smooth pursuit eye movements in a given portion of trials, on the accuracy and timing of pursuit. Insights into the temporal dynamics of reward effects can further our understanding of the brain mechanisms underlying the integration of reward information with visual-motor processing.

Reward effects on behavioral choices

Most human behavior is driven by the desire to maximize its expected outcome or value. In the past decade, neurobiological studies in non-human primates and imaging studies in humans have significantly advanced our understanding of how reward information is processed in the brain and how it affects behavior (e.g., Glimcher, 2003; Hare, Schultz, Camerer, O'Doherty & Rangel, 2011; Hunt et al., 2012; Kable & Glimcher, 2009; Padoa-Schioppa & Assad, 2006; Rangel & Hare, 2010; Schultz, 2006). Behavioral studies in decision-making have shown that expected reward facilitates and biases goal-oriented behavior, such as eye or hand movements, towards the location or object associated with a higher reward. In a typical experimental situation in the laboratory, two visual stimuli appear in different locations but only one location is associated with a reward (e.g., food,

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money or points). In a binary choice task, observers have to select a location by making an eye or hand movement towards it as quickly and accurately as possible. In these studies, the eye or hand is directed more often towards the rewarded location than towards the unrewarded location (Sohn & Lee, 2006; Schütz, Trommershäuser & Gegenfurtner, 2012; Takikawa, Kawagoe, Itoh, Nakahara & Hikosaka, 2002; Theeuwes & Belopolsky, 2012). For instance, Schütz and colleagues (2012) developed a saccade paradigm to trade off visual salience against expected value and showed that both kinds of information are integrated to guide motor responses. Theeuwes and Belopolsky (2012) found that associating a task-irrelevant stimulus (distractor) with reward changed the distractor's salience, leading to a higher number of saccades towards the distractor. Moreover, humans efficiently adjust motor responses to maximize expected outcomes. Trommershäuser, Landy and Maloney (2006) asked participants to rapidly point at a stimulus configuration of two interlocking circles, one defined as a reward region, where observers could earn points, the other defined as a penalty region, where observers would lose points. Participants rapidly and optimally adjusted reaching behavior to maximize reward.

In recent years, psychological studies in humans have shown that reward not only affects motor behavior, but also increases visual sensitivity (Pascucci & Turatto, 2013; Seitz, Kim & Watanabe, 2009), biases target selection in visual search (Kiss, Driver & Eimer, 2009, Anderson & Yantis, 2013), and affects visual selective attention (Anderson, Laurent & Yantis, 2011; Della Libera & Chelazzi, 2006; Hickey, Chelazzi & Theeuwes, 2010; Raymond & O'Brien, 2009).

Reward effects on movement kinematics and reaction time

Whereas these studies investigated effects of reward on choice behavior and showed that reward can bias perceptual and motor responses, other studies have assessed reward effects on motor processing itself. Reward facilitates movements, leading to shorter and less variable reaction times in saccadic eye movements (Ikeda & Hikosaka, 2003; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002;

Madelain, Champrenaut & Chauvin, 2007; Milstein & Dorris, 2007; Takikawa et al., 2002; Watanabe, Lauwereyns & Hikosaka, 2003) and manual responses (Madelain et al., 2007). Saccades to rewarded locations also have shorter durations and higher peak velocities than saccades to unrewarded locations (Hikosaka, 2007; Takikawa et al. 2002; Xu-Wilson, Zee & Shadmehr, 2009), indicating that reward not only affects choices but also modulates the execution of motor behavior in choice situations.

Reward effects on movement dynamics

How fast does reward affect visual-motor processing and behavior? On the one hand, studies manipulating the prior experience of reward (reward history) reveal relatively fast effects situated at low processing levels. Physiological studies in rodents (e.g., Shuler & Bear, 2006) and imaging studies in humans (e.g., Serences, 2008) show that reward history can modulate activity early along the cortical visual processing hierarchy, in primary visual cortex (V1). Stanisor and colleagues (Stanisor, van der Togt, Pennartz, & Roelfsema, 2013) trained monkeys to trace a target curve and ignore a distractor curve, each associated with different reward values at the end of the curve. These authors found that the difference between target curve value and distractor curve value modulated V1 neuronal activity. Recent reward history can also bias short-latency saccades towards previously rewarded locations. Hickey and van Zoest (2012) asked observers to make a saccade towards a target while ignoring a distractor that was previously associated with a reward. Even though observers had full knowledge about whether and where the distractor would appear, trajectories of short-latency saccades (mean latency 152 ms) were biased towards previously rewarded distractors, and long-latency saccades (267 ms) were biased away from them.

On the other hand, studies manipulating reward probability (reward prospect) usually reveal slower effects. For instance, Schütz and colleagues (2012) found larger effects of reward on long-latency saccades (>184 ms) than on short-latency saccades (~150 ms), indicating that reward effects

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take more time to evolve than the shortest latencies of saccades. Saccade latencies, which are usually in the range of 150-300 ms (with the exception of express saccades), only allow a relatively coarse resolution of temporal dynamics.

Reward effects on smooth pursuit accuracy and dynamics

In this study, we took advantage of the continuous nature of smooth pursuit eye movements to assess the temporal dynamics of reward effects at a finer resolution. Smooth pursuit can be separated into two response phases: an initial ("open-loop") phase, driven by visual (retinal) motion signals (Tychsen & Lisberger, 1986; Lisberger, 2010), and a later ("closed-loop") phase, driven by a combination of retinal and extra-retinal signals, such as efference-copy feedback information (Lisberger, 2010; Spering & Montagnini, 2011). Effects of expected reward on open-loop pursuit would indicate modulations at early stages of visual-motor processing. Effects of expected reward on closed-loop pursuit would indicate modulations of visual-motor processing at the gain-control and feedback stage. Changes across the entire pursuit response would indicate a broad integration of reward information across the sensorimotor control system.

We implemented a paradigm in which human smooth pursuit eye movements to a single visual target were associated with an expected reward in some trials, and unrewarded in others. An important distinction to be made in the reward literature is whether reward is indicated by a pre-cue (e.g. Glimcher, 2003; Padoa-Schioppa & Assad, 2006; Hare et al., 2011; Serences, 2008; Shuler & Bear, 2006; Stanisor et al., 2013) or whether it is directly associated with a particular target feature or target location (e.g. Anderson et al., 2011; Anderson & Yantis, 2013; Della Libera & Chelazzi, 2009; Gottlieb, Hayhoe, Hikosaka & Rangel, 2014; Hickey et al., 2010; Hickey & van Zoest, 2012; Hikosaka, 2007; Joshua & Lisberger, 2012; Milstein & Dorris, 2007; Pascucci & Turatto, 2013; Peck, Jangraw, Suzuki, Efem & Gottlieb, 2009; Raymond & O'Brien, 2009; Schütz et al., 2012; Seitz et al., 2009; Takikawa et al., 2002; Theeuwes & Belopolsky, 2012; Xu-Wilson et al., 2009). We

compared pursuit in both types of paradigms in which reward was either indicated by a precue or associated with the pursuit target's color. Moreover, many reward studies acknowledge that they cannot distinguish between effects of reward and those of attention or motivation (Maunsell, 2004; Roesch & Olson, 2007; Serences, 2008). We performed experiments to assess differential effects of reward and enhanced motivation or preparation.

General methods

We conducted four experiments; experiments 2-4 were variations of experiment 1 but differed with regard to visual pursuit stimulus (experiments 2,3) or type of cue (experiment 4). Apparatus, eye movement recording methods, and data analysis were identical for all experiments. General methods apply to experiment 1; changes to these procedures, where applicable, are described in each experiment's section.

Participants

Participants in experiment 1 were 11 individuals (mean age = 24.6 years, *SD* = 4.3, 6 females) with normal and uncorrected visual acuity, untrained and unaware of the study's hypotheses. Study procedures were approved by UBC's Behavioral Research Ethics Board and subjects participated with written informed consent. Remuneration was $10 per hour plus a bonus of $12 earned in reward trials; this amount was fixed and independent of participants' performance.

Apparatus and visual stimuli

Stimuli were shown on a 21-in. calibrated CRT monitor (Viewsonic G225f, 85-Hz refresh rate, 1,600 x 1,200 pixels; 40.7 wide x 30.3 cm high). Stimulus presentation and data acquisition were controlled by a Windows PC running Matlab Psychophysics Toolbox 3 and the Matlab Data Acquisition Toolbox (The MathWorks, Natick, MA). The fixation target was a red cross with diameter 0.6°. The pursuit target was a white spot, 0.3° in diameter, presented at 100% contrast (96

cd/m^2) on a uniform grey background (48 cd/m^2). The target moved horizontally to the left or right at a constant speed of 10°/s. Reward cues were images of Canadian 5- and 25-cent coins, each scaled to 150 x 150 pixels and grayscale-adjusted to equal luminance (52 cd/cm^2). Participants viewed the display from a distance of 92 cm with their head stabilized by a chin- and forehead rest.

Procedure and design

We compared pursuit performance in trials in which observers could either earn or could not earn a monetary reward. Each trial started with a reward cue (**Fig. 1a**) indicating a reward trial (25-cent coin) or a no-reward trial (5-cent coin); showing a cue in both conditions allowed us to keep visual stimulation constant across conditions. Following a random fixation interval the pursuit target appeared in the center and moved across the monitor to the left or right. The stimulus was initially displaced in the direction opposite to the target's velocity by 2° (the "step") before moving back across the fovea for 1,024 ms (the "ramp"). This step-ramp procedure (Rashbass, 1961) is commonly used in smooth-pursuit laboratory studies to prevent early saccades in the direction of stimulus motion and to allow assessment of smooth pursuit initiation. Participants were instructed to track the moving target accurately with their eyes. They were informed that they would earn 25 cents for accurate tracking in each reward trial and no money in trials with a no-reward cue; the ratio of reward to no-reward trials was 1:4 in each block of trials. Participants did not earn money in no-reward trials to create conditions as different in expected reward as possible. Note that tracking accuracy was not measured online during a given trial; instead, participants received 25 cents for each reward trial at the end of the experiment.

In each experiment, we aimed at collecting a total of 320 trials in 4 blocks per participant, in sessions lasting no longer than 60 minutes. Eye-tracker set up and calibration duration varied between participants due to individual differences in facial and eye anatomy. Hence, numbers of blocks per subject varied. In experiment 1, eight participants completed three blocks of 80 trials and

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three participants completed four blocks, resulting in a total of 2,880 trials across participants (536 reward, 2,304 no reward).

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Figure 1 here
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Eye movement recordings and data processing

In all experiments, eye position of the right eye was recorded with a Dual Purkinje image eye tracker (Gen. 5, Fourward Technologies, Gallatin, MO) at a sampling rate of 1 kHz and converted to digital signals. Eye movements were analyzed off-line using Matlab. Eye velocity was obtained by differentiation of eye position signals over time, and smoothed with a low-pass filter (40 Hz cut-off). Saccades were detected based on eye acceleration, obtained by differentiating unfiltered eye velocity; 20 consecutive samples had to exceed an acceleration of $300°/s^2$ to be counted as saccade samples. For the analysis of smooth pursuit, saccades were removed from position and velocity traces. Smooth eye movement onset was detected in the initial 300-ms interval after stimulus motion onset using a piecewise linear fit to 2D eye position traces. The least-squares error of the fitted model was minimized iteratively until a fixed criterion was reached, indicating the time of pursuit onset. If a saccade occurred in the open-loop interval, the interval's end was defined as the onset of smooth pursuit. The minimum open-loop window length was 75 ms; trials with a shorter open-loop period due to an early saccade were removed from all analyses. We analyzed the latency of the pursuit response and the time at which pursuit reached its peak acceleration as indices of temporal dynamics of reward effects. To assess accuracy of open-loop pursuit, we analyzed mean eye acceleration averaged across the initial 140 ms of the pursuit response. For accuracy of closed-loop pursuit, we calculated velocity gain (mean eye velocity across the interval 200-400 ms after pursuit onset divided by target velocity) and velocity error (root mean square difference between eye and target velocity across the entire stimulus motion interval). The frequency and amplitude of catch-up saccades were used as indices of pursuit smoothness. We excluded trials with blinks, trials in which the tracker lost

the signal, trials without smooth pursuit onset, or trials with early saccades in the first 75 ms of pursuit (20% of trials excluded in experiment 1).

Statistical analysis

Eye movement data were entered into a one-way repeated measures analysis of variance (ANOVA) with reward as factor. To investigate effects of reward independent of differences in effect magnitude between subjects and experiments we calculated a reward index as the difference between means in reward versus no-reward trials divided by the sum of means. Reward index (RI) was calculated for each eye movement parameter, for instance, eye velocity gain:

$$RI_{gain} = (gain_{reward} - gain_{no\ reward}) / (gain_{reward} + gain_{no\ reward}).$$

Results

Smooth pursuit eye movements were more accurate in trials in which observers expected to receive a monetary reward than in trials in which they expected no reward. **Figure 2** shows mean eye-velocity traces for reward (black traces) and no-reward trials (gray traces) for three representative observers. All observers showed higher pursuit velocity in reward trials despite expected individual differences in overall pursuit quality.

Figures 2 and 3 here

Across all observers, reward improved pursuit accuracy across the entire pursuit response, significantly increasing open-loop acceleration by 9% (**Table 1** and **Fig. 3a**) and closed-loop velocity gain by 4% in reward as compared to no-reward trials (**Table 1** and **Fig. 3b**). Thus, reward significantly enhanced the early approximation of target velocity in the open-loop phase and the match between closed-loop eye velocity and target velocity (note that a gain of 1 implies perfect target tracking). Accordingly, the overall velocity error was 14% lower in reward compared to no-reward trials (**Table 1**, **Fig. 3c**). Although reward improved pursuit accuracy, it did not reduce pursuit

latency. We next tested whether this could have been due to delays in processing the reward cue and calculated the time at which peak acceleration was reached during the open-loop phase. Reward did not affect the time at which the eye reached its peak acceleration despite significant reward effects on open-loop acceleration itself. This finding indicates that the null-effect on latency cannot be due to delays in cue processing. Fewer catch-up saccades were made in reward trials than in no-reward trials (11% lower catch-up saccade rate), but this difference was not significant (**Table 1**).

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Table 1 here

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Experiment 2: Reward enhances pursuit accuracy at low luminance contrast

To investigate whether our finding that reward increases pursuit accuracy across the open-loop and closed-loop phase (but does not reduce latency) holds across different levels of task difficulty we repeated experiment 1 at low luminance contrast. We previously showed that smooth pursuit is significantly impaired (longer latencies, lower acceleration and velocity) at low luminance contrast (Spering, Kerzel, Braun, Hawken & Gegenfurtner, 2005). Here, we reduced pursuit target luminance to 68 cd/m^2, resulting in a Weber contrast of approx. 42%; all procedures were identical to experiment 1. We tested 11 participants (mean age=26.6 years; *SD*=6.8; 8 females) who, depending on duration of set-up and calibration, completed either three (*n*=4) or four blocks (*n*=7) of 80 trials each, resulting in 3,200 trials total. We excluded 19% of trials from pursuit analysis following criteria outlined in General Methods.

Results

We compared results from experiments 1 and 2 in a 2x2 repeated-measures ANOVA with reward as within-subjects factor and contrast (experiment) as between-subjects factor. Experiment 2 replicated reward effects from experiment 1, although target tracking was more difficult at low contrast (main effects of contrast on latency, velocity error and saccade amplitude; **Table 2**).

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However, reward still significantly improved open-loop and closed-loop pursuit measures with a 7% increase in acceleration ($F(1,10)=9.17$, $p=.01$, $d=0.22$) and a 5% increase in gain ($F(1,10)=6.43$, $p=.03$, $d=0.40$) in reward as compared to no-reward trials (results from a one-way repeated measures ANOVA with factor reward). As in experiment 1, participants made 8% fewer catch-up saccades in reward trials, but this difference was non-significant ($F(1,10)=2.69$, $p=.13$, $d=-0.44$). Speed-of-processing measures latency and time of peak were not affected by reward (both $F<1$).

Experiment 3: Reward effects are not due to enhanced preparation or stimulus prevalence

Reward effects in experiments 1-2 were triggered by cues prior to the onset of the pursuit target. These precues indicate the availability of reward, but may simultaneously elicit an increase in mental preparation or motivation. Preparation, based on cognitive expectations about the location, time, identity or features of events, increases the speed and accuracy of responses to sensory stimuli in general (reviewed in Jennings & van der Molen, 2005) and impacts visual perception (Rohenkohl Gould, Pessoa & Nobre, 2014; Vangkilde, Coull & Bundesen, 2012) and smooth pursuit eye movements in particular (for reviews see Barnes, 2008; Kowler, 2011). An alternative way to manipulate reward is to associate it implicitly or explicitly with a target feature or the target location.

In experiment 3 we manipulated stimulus color (green or yellow, adjusted to an equal luminance of 69 cd/m^2) to explicitly associate reward with the pursuit target. Participants ($n=16$, mean age=30.1 yrs, $SD=9.2$, 10 females) were randomly assigned to one of two experiment versions.

In experiment 3a (**Table 3**; **Fig. 1b**), participants were told that they could earn 25 cents for accurately tracking the green target, while trials with the yellow target would be unrewarded (1:4 ratio). Prior to running this experiment participants completed a block of 20 practice trials to learn

the reward association. In those practice trials, a coin image was shown after tracking the green target and a gray circle was shown after tracking the yellow target.

In experiment 3b (**Table 3**; **Fig. 1b**), participants were instructed to track the green or yellow target without any indication of reward. Critically, we used the same 1:4 frequency ratio of green to yellow as in experiment 3a, allowing us to control for effects of stimulus prevalence. In experiments 1-3a, the less prevalent cue or stimulus was always paired with reward and the more prevalent cue or stimulus was paired with no reward. Stimulus prevalence may result in higher assigned value and/or salience, and hence, enhance visual processing (e.g., Foley, Jangraw, Peck & Gottlieb, 2014). If target color affects pursuit parameters in experiment 3a, but not in 3b, effects cannot be attributed to prevalence but to reward alone.

All participants completed four blocks of 80 trials (5,120 trials total); 36% of trials were excluded from analyses. All participants received a remuneration of $15 regardless of which experiment version they were assigned to.

Results

Experiment 3a replicated results from experiments 1-2 and showed significantly improved pursuit quality in reward vs. no reward trials (**Fig. 4**, left bars): eye acceleration increased by 3% ($F(1,7)=6.01$, $p=.04$, $d=0.29$; **Fig. 4a**), velocity gain increased by 9% ($F(1,7)=36.65$, $p=.001$, $d=1.67$; **Fig. 4b**), velocity error decreased by 18% ($F(1,7)=21.46$, $p=.002$, $d=-1.05$; **Fig. 4c**) and the number of catch-up saccades was reduced by 20% ($F(1,7)=15.31$, $p=.006$, $d=-0.85$; **Fig. 4d**). As in experiments 1-2, measures of pursuit timing were unaffected (all p=n.s.).

In experiment 3b, performance did not differ significantly between trials with low-prevalence (green) vs. high-prevalence (yellow) target for any of the open-loop or closed-loop pursuit parameters (all p=n.s.; **Fig. 4**, right bars).

We compared results across experiments 3a and 3b to assess the reliability of the difference between low-prevalence stimuli associated with reward (3a) vs. no reward (3b). A 2x2 repeated-measures ANOVA with stimulus prevalence (color) as within-subjects factor and experiment as between-subjects factor showed significant prevalence X experiment interactions for pursuit acceleration ($F(1,14)$=5.2, p=.04, **Fig. 4a**), gain ($F(1,14)$=14.6, p=.002, **Fig. 4b**), velocity error ($F(1,14)$=8.7, p=.01, **Fig. 4c**) and saccade number ($F(1,14)$=6.9, p=.02, **Fig. 4d**). Bonferroni-corrected post-hoc comparisons confirmed that stimulus prevalence only affected pursuit parameters in experiment 3a (all p≤.05), but not experiment 3b (all p=n.s.) These findings indicate that stimulus prevalence did not affect pursuit, and that effects in experiments 1-3a may be attributed to reward alone.

Figure 4 and Table 3 here

Taking advantage of the identical procedures in experiments 3a and 3b we next assessed whether reward effects were either due to (1) positive effects/benefits of expecting a reward, or (2) negative effects/costs of not expecting a reward. We compared results across experiments 3a and 3b within one color category (within rows in **Table 3**). If observed differences are due to benefits of reward we would expect better pursuit to the high-prevalence, green target in experiment 3a (reward) than in experiment 3b (no instruction) and equal performance for low-prevalence, yellow targets across experiments. Conversely, if effects were due to costs of no reward we would expect worse pursuit to the low-prevalence, yellow target in experiment 3a (no reward) than in experiment 3b (no instruction) and equal performance for high-prevalence, green targets across experiments. We performed independent sample t-tests to compare pursuit parameters for one target color between experiments. Pursuit was better in low-prevalence rewarded trials (exp. 3a) than in low-prevalence trials without instruction (exp. 3b); compare black bars across experiments in **Figures 4a-d** (and see **Table 3**). This difference reached significance for gain (p=.04, d=.97) but not for acceleration (p=.42,

d=.10), velocity error (*p*=.12, *d*=-.60) and saccade number (*p*=.06, *d*=-.84), but note medium to large effect sizes for velocity error and saccade number. We found no significant difference between yellow-target trials across experiments for any pursuit parameter (all *p*=n.s.); compare grey bars across experiments in **Figures 4a-d** (and see **Table 3**). These results are in line with the hypothesis that differences between reward and no-reward trials are due to benefits of reward.

Figure 5 here

To summarize: a comparison of reward indices across all observers in experiments 1-3a confirmed consistent and significant reward effects (**Fig. 5**). Clustering of data points above the diagonal in **Figures 5a, 5b** indicates increased acceleration and velocity gain in reward trials, clustering below the diagonal in **Figure 5c** indicates a decrease in velocity error in reward trials and thus improved pursuit performance. No difference was observed for latency (**Fig. 5d**).

Experiment 4: No reward effect following numerical reward cues

Many studies assessing expected reward in humans have used numerical cues, indicating the number of points gained when choosing a particular location, stimulus or behavior; points are translated into monetary rewards (e.g., Hickey et al., 2010; Kiss et al., 2009; Trommershäuser et al., 2006). To assess whether reward effects generalize to abstract cues, participants in experiment 4 were briefly presented numbers ("25" or "0") as cues before stimulus onset, indicating a reward or no-reward trial; participants were told that 25 points would translate to 25 cents thus linking the same actual reward to reward trials as in experiments 1 and 2. All stimuli and procedures, as well as reward contingencies, were identical to experiment 1. Nine participants completed three or four blocks of 80 trials each, resulting in 2,870 trials total (one block terminated early); 37% of all trials were excluded from pursuit analysis.

Results

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Reward did not impact pursuit when indicated by a numerical cue (all p=n.s.; **Fig. 6**).

Additional control experiments (data not shown) ruled out that this null effect was due to the use of small numbers or to including a 0-point condition. We found no reward effects when repeating the experiment (n=6) with a larger-number reward cue ("1000"), translating to the same monetary reward of 25 cents. We further found no reward effects when repeating the experiment (n=6) with three conditions – 0, 100, and 1000 points in a 40:40:20 ratio. If including a 0-point condition had affected our results we should have still observed differences between then "100" and "1000" cue conditions.

Figure 6 here

A comparison between results from experiments 1 and 4 in a 2x2 repeated-measures ANOVA with reward as within-subject factor and cue type (experiment) as between-subject factor showed significant reward X experiment interactions for pursuit gain ($F(1,18)$=6.6, p=.02) and eye velocity error ($F(1,18)$=5.9, p=.03). The interaction did not reach significance for acceleration ($F(1,18)$=3.8, p=.06), despite differences in effects between experiments (compare **Fig. 3a** and **Fig. 6b**) In sum, these findings indicate that the difference between cue types – monetary vs. numerical – has a significant impact on performance, especially during the later pursuit phase.

General discussion

The present study investigated the effects of reward on the timing and accuracy of smooth pursuit eye movements and reports several key findings.

(1) Eye movements were more accurate in trials in which observers expected to receive a reward than in trials in which they did not expect a reward. These findings indicate that reward directly improves visual-motor processing for the execution of eye movements.

(2) Improvements in pursuit accuracy were observed across the entire pursuit response –in the visually-driven open-loop phase and the later, feedback-modulated closed-loop phase. Effects on the earliest phase of the pursuit response suggest that reward affects visual-motor processing early in the cortical hierarchy, where visual motion information is encoded for a later transformation into motor commands.

(3) Reward did not improve pursuit timing. The fact that reward increased peak acceleration, but did not affect the time at which peak acceleration was reached, suggests that the null-effect on timing cannot result from temporal delays in reward cue processing alone (see also experiment 3a, replicating these results in a design in which the pursuit target was directly associated with reward). Based on these results, we hypothesize that reward may have differential effects on the processing speed and the read-out quality of the visual motion signal.

(4) Reward effects were found regardless of whether reward was precued (experiments 1-2) or associated with a target feature (experiment 3a), indicating that observed differences between reward and no-reward trials were not due to enhanced motivation, preparation or stimulus prevalence.

(5) Reward only impacted pursuit if monetary reward cues rather than numerical cues were utilized (experiment 4). The two cue types differ with regard to their inherent incentive value (Berridge & Robinson, 2003) –the strength of the association between cue and actual reward paid out to the participant– and their emotional valence. However, these null-effects cannot be explained by differences in cue abstractness, because strong reward effects were also found in experiment 3a, where stimulus color indicated reward. Rather, these results may be due to a decay of reward/value effects over time (e.g. Shadmehr, Orban de Xivry, Xu-Wilson & Shih , 2010), indicating that only cues with high intrinsic value or strong positive valence may sustain over a period of >1 second.

Reward modulates pursuit initiation and maintenance

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Whereas effects of reward on saccadic target selection and saccade dynamics are well documented, to our knowledge, only one study has investigated the effect of reward on choice behavior in smooth pursuit eye movements. Joshua and Lisberger (2012) trained three monkeys to track one of two possible targets which moved into orthogonal directions, each associated with a different reward size. Initial pursuit direction was biased towards the target motion direction associated with the larger reward, linking this study to an existing body of literature on target selection in pursuit (Garbutt & Lisberger 2006; Lisberger & Ferrera, 1997; Spering, Gegenfurtner & Kerzel, 2006). However, when monkeys tracked single targets, only modest reward effects on initial eye acceleration, steady-state velocity and number of catch-up saccades were described qualitatively; other open-loop and closed-loop pursuit parameters were not reported in that study. The authors conclude that the site of reward modulation is downstream from sensory visual processing. In contrast, we found statistically significant reward effects of medium to large effect size, consistent across observers, on open-loop eye acceleration, closed-loop gain, eye velocity error and saccade number (in experiment 3a). Significant reward effects were obtained regardless of whether reward was pre-cued (experiments 1-2) or whether it was explicitly associated with pursuit target color (experiment 3a). The difference in findings between our study and Joshua and Lisberger (2012) can potentially be explained by the fact that monkeys used in laboratory eye-movement tasks are highly trained and hence only small improvements can be achieved.

Critically, we found significant effects of reward on initial peak eye acceleration, reached within approx. 70 ms of eye movement onset. At that point in time, the smooth pursuit response is assumed to be purely visually driven (Lisberger, 2010; Tychsen & Lysberger, 1986). Higher-level signals such as visual spatial attention, for instance, only have small effects on early pursuit (Barnes, 2008; Lee & Maunsell, 2010; Souto & Kerzel, 2008), reflected in the time it takes for attention to modulate MT neuronal activity (Recanzone & Wurtz, 2000).

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Neural correlates of reward effects on pursuit

Significant early reward modulations of smooth pursuit eye movements suggest that reward may enhance the processing of low-level visual information, such as the direction and speed of a visual object. Such modulations would likely occur early along the visual processing pathways, in V1 and the middle temporal visual area (MT/V5). Neuronal responses in area MT, tuned to the direction and speed of a visual object, are the major source of the visual motion signals driving smooth pursuit (Groh, Born & Newsome, 1997; Lisberger & Movshon, 1999; Lisberger, 2010; Newsome, Wurtz, Dürsteler & Mikami, 1985). Reward effects at this processing stage may modulate the gain and sensitivity of neurons. For instance, an increased open-loop pursuit response in reward trials may correspond to a higher firing rate or narrower tuning width of MT neurons.

Expected reward may also improve the read-out of visual motion information in areas that carry both sensory and motor signals, resulting in changes in the transformation of visual signals into ocular-motor commands. This model is consistent with recent neurophysiological and imaging studies revealing reward-based modulations in early visual cortical areas (Serences, 2008; Shuler & Bear, 2006; Stanisor et al., 2013). As one possible candidate the pursuit region of the frontal eye fields (FEF) has been associated with gain modulations of the visual-motor transformation (MacAvoy, Gottlieb & Bruce, 1991; Schwartz & Lisberger, 1994). Area FEF has also been linked to effects of reward (Ding & Hikosaka, 2006; Leon & Shadlen, 1999; Roesch & Olson, 2003). Moreover, FEF neurons project to the basal ganglia, where neurons sensitive to reward (Ding & Hikosaka, 2006; Gottlieb et al., 2014; Hikosaka, 2007; Lauwereyns et al., 2002) as well as pursuit (Basso, Pokorny & Liu, 2005) have been found. Microstimulation of pursuit neurons in area FEF results in larger velocity responses during pursuit than during fixation (Tanaka & Lisberger, 2001). Hence, an increased pursuit response in reward trials –higher open-loop acceleration and closed-loop velocity gain– may correspond to a higher firing rate in FEF neurons, and potentially in downstream

motor areas. Furthermore, improvements of pursuit gain in reward trials may result from changes to the functioning of the efference-copy signal –information about ongoing pursuit velocity used to maintain steady-state pursuit, even in the absence of visual image motion. Pursuit efference-copy signals have been found in some of the same brain regions that are also associated with reward effects, such as area FEF.

Does reward modulate pursuit directly or via effects on attention?

Effects of reward and visual selective attention are widespread across the brain, with parallel representations in many brain areas ranging from occipital to fronto-parietal areas. Generally, reward and attention both lead to a selective enhancement of responses in those neurons that represent the rewarded or attended stimulus or location. For instance, neuronal activity in area MT may be modulated by reward in much the same way as has been reported for feature-based attention (Martinez-Trujillo & Treue, 2004) and spatial attention (Womelsdorf, Anton-Erxleben, Pieper & Treue, 2006). Whereas some studies have shown independent neuronal signatures of reward and attention (e.g., Peck et al., 2009; Tosoni, Shulman, Pope, McAvoy & Corbetta, 2013), others have revealed similarities in magnitude and time course of reward and attention effects in primary visual cortex (Stanisor et al., 2013) and in area FEF (Ding & Hikosaka, 2006). Neuronal activity in other areas, such as the posterior cingulate cortex (Tosoni et al., 2013), the caudate nucleus (Ding & Hikosaka, 2006), the lateral intraparietal area (LIP; Peck et al., 2009), the ventral striatum, ventral tegmental area and fusiform gyrus (Rothkirch, Schmack, Deserno, Darmohray & Sterzer, 2014) showed differential signatures of reward and attention. However, in all studies in which cues provide information about reward magnitude, behavioral effects of reward and attention may be difficult to distinguish (Maunsell, 2004): A higher reward could merely lead to a heightened state of attention. Our study was not designed to address differential effects of reward and attention. However, there is agreement in the literature that smooth pursuit critically requires the allocation of visual spatial

attention to the pursuit target (Khurana & Kowler, 1987; Lovejoy, Fowler & Krauzlis, 2009). Attention shifts away from the pursuit target result in decreased velocity gain (Madelain, Krauzlis & Wallman, 2005), even though effects on open-loop tracking are small (Souto & Kerzel, 2008). Given the tight coupling between attention and pursuit target, we assume that any beneficial effects of reward on pursuit accuracy must be over and above those of attention, which should be constant during pursuit.

Does reward modulate pursuit via effects on motivation?

Motivational effects likely interact with reward to influence neuronal activity in cortical and subcortical brain areas that also control smooth pursuit, for instance, frontal cortex (Basten, Biele, Heekeren & Fiebach, 2010; Hare et al., 2011; Roesch & Olson, 2007), basal ganglia (Kawagoe, Takikawa & Hikosaka, 1998), and the superior colliculus (Ikeda & Hikosaka, 2003). In studies manipulating reward expectations, the level of motivation, attentional engagement or attentional intensity (Dijksterhuis & Aarts, 2010; Ivanov et al., 2012; Padmala & Pessoa, 2011), can be expected to be correlated with the amount of expected reward in a given trial. Heightened motivation or attentional engagement would be expected to lead to a general up-regulation of perceptual abilities and neuronal processing (Padmala & Pessoa, 2011), thereby improving smooth pursuit in our task.

This is a concern in experiments 1, 2 and 4, where a cue prior to target motion onset signaled reward and could indeed have triggered such an up-regulation of processing. In experiment 3a, however, where the pursuit target itself was directly associated with the possibility to earn a reward, no change in motivation or preparedness could have taken place prior to target motion onset. Results in this experiment replicate findings in experiments 1 and 2, indicating that any potential increase in motivation in these experiments cannot explain reward effects.

To conclude, our findings indicate that the accuracy of eye movements can be significantly improved by linking them with an expected reward, if effective reward cues are used. We show that pursuit sensitively reflects benefits of higher expected reward even in the earliest phase of the motor response, indicating that reward effects act at early stages of visual-motor processing in the brain. We obtained these results by taking advantage of the continuous nature of smooth pursuit eye movements, a powerful tool to investigate visual and cognitive processes, such as attention, expectation, prediction and working memory (Barnes, 2008). Our findings significantly advance our understanding of the cognitive factors that drive goal-directed eye movements such as smooth pursuit.

Acknowledgements

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Tables

Table 1. Main effects of reward on pursuit measures in experiment 1 in a one-way repeated-measures ANOVA.

	Reward condition						
	Reward		No reward				
	M	*SD*	*M*	*SD*	*F*(1,10)	η^2	*P*
Acceleration (deg/s²)	61.83	12.91	56.56	9.49	6.76	0.40	**.03**
Velocity gain	0.97	0.10	0.93	0.12	6.56	0.40	**.03**
Velocity error (deg)	2.98	0.96	3.45	1.06	9.24	0.48	**.01**
Latency (ms)	132.30	20.22	131.81	16.23	0.03	0.00	.86
Time of peak accel. (ms)	73.63	8.82	72.61	7.43	0.31	0.03	.59
Saccade number	1.69	0.82	1.90	0.68	2.08	0.17	.18
Saccade amplitude (deg)	1.46	0.47	1.56	0.44	1.72	0.20	.76

Note. Numbers in bold denote significant results.

Table 2. Main effects of reward, contrast and their interaction in a 2 x 2 (reward x contrast) ANOVA comparing experiments 1 and 2.

	Reward			Contrast			Reward x Contrast		
	$F(1,20)$	η^2	*p*	$F(1,20)$	η^2	*p*	$F(1,20)$	η^2	*p*
Acceleration (deg/s²)	14.50	.42	**.001**	1.21	.06	.28	0.36	.02	.55
Velocity gain	13.34	.40	**.002**	0.14	.01	.71	0.04	.00	.84
Velocity error (deg)	10.17	.34	**.005**	6.90	.26	**.02**	1.41	.07	.25
Latency (ms)	0.13	.01	.72	77.56	.80	**<.001**	0.01	.00	.92
Time of peak accel. (ms)	0.02	.00	.88	0.60	.03	.45	0.55	.03	.47
Saccade number	4.21	.17	**.05**	0.07	.00	.80	0.23	.01	.64
Saccade amplitude (deg)	2.94	.13	.10	7.04	.26	**.02**	1.71	.08	.21

Table 3. Design and results in experiments 3a and 3b. Comparisons within columns reveal effects of reward (exp. 3a) or prevalence (exp. 3b); comparisons within rows allow contrasting benefits associated with reward vs. cost associated with no reward (">" indicates better performance, "=" indicates equal performance).

	Experiment 3a	*Performance*	*Experiment 3b*
Green target (20% trials)	Reward	>	No reward instruction
Performance	∨		‖
Yellow target (80% trials)	No reward	=	No reward instruction
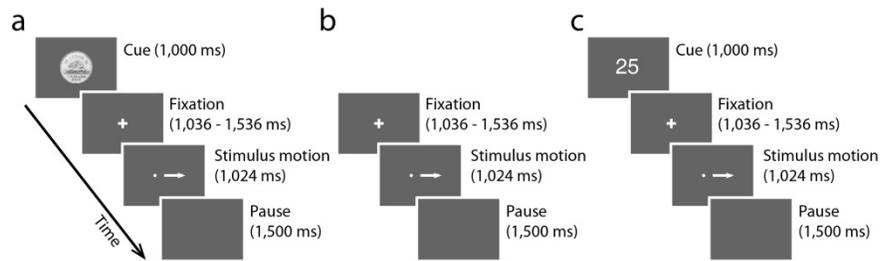
Figure 1. Trial timeline for one example trial for each experiment. **(a)** Experiments 1 and 2 used coins as reward cues; trial timeline for a reward trial (25-cent coin). **(b)** Experiment 3a associated reward with stimulus color (green); experiment 3b assessed effects of tracking colored targets (green vs. yellow) without reward association. Colored target shown in white for illustration purposes. **(c)** Experiment 4 used numbers as reward cues; trial timeline for a reward trial ("25" displayed). All fixation targets shown in white for illustration purposes.
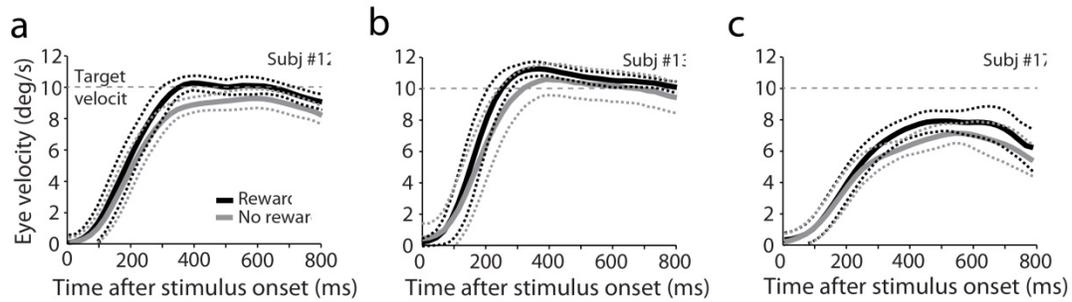
Figure 2. Mean eye velocity traces for reward (black line) and no-reward trials (gray line) for three representative participants. Mean traces were derived from filtered eye-velocity traces in which eye velocity during saccades was replaced by linear interpolation. Dotted lines indicate standard deviations.
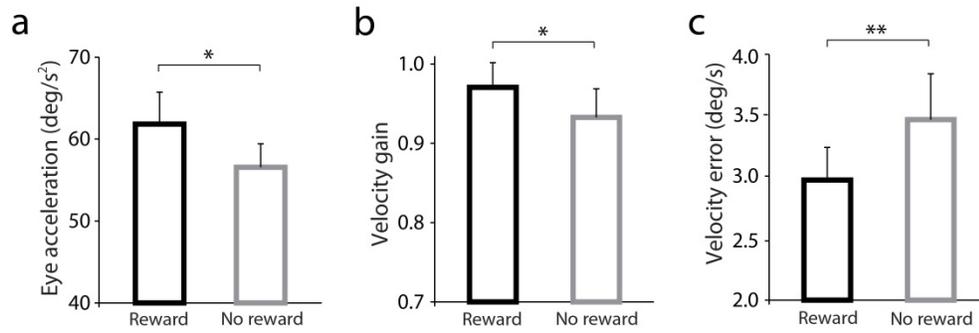
Figure 3. Effects of reward on open-loop and closed-loop pursuit in experiment 1 (*n*=11). **(a)** Mean open-loop eye acceleration. **(b)** Mean closed-loop velocity gain. **(c)** Mean velocity error. Error bars denote standard errors. Asterisks denote significance, *p*<.05, **p*<.01.
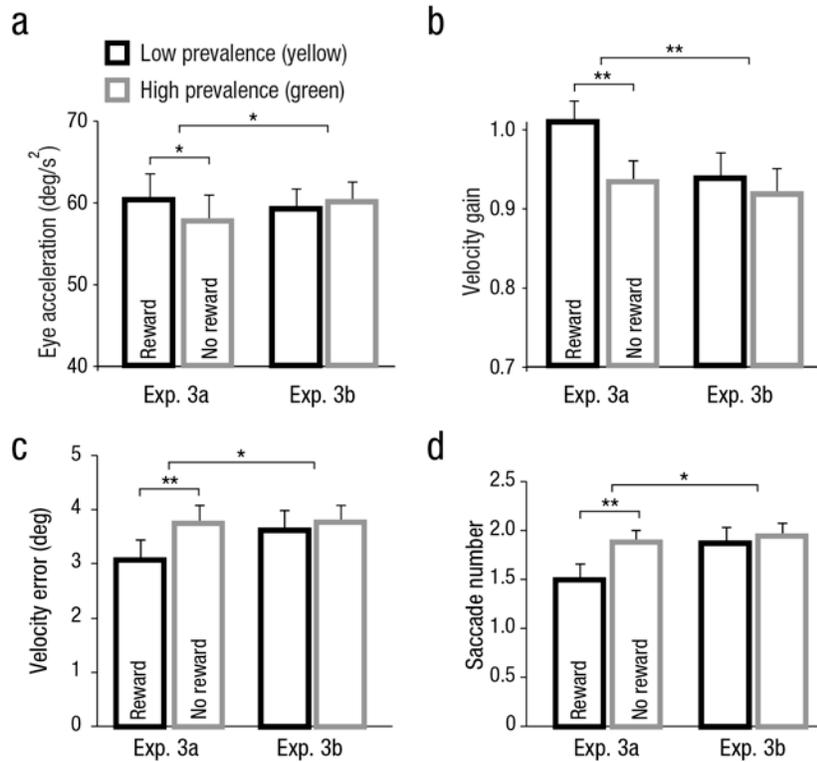
Figure 4. Effects of reward and stimulus prevalence in experiment 3. Means are shown

separately for experiment 3a (left side of each graph, *n*=8), and experiment 3b (right side, *n*=8).

(a) Open-loop eye acceleration. **(b)** Closed-loop velocity gain. **(c)** Velocity error. **(d)** Saccade

number. Error bars denote standard errors. Asterisks indicate significant differences between

reward conditions in experiment 3a and significant prevalence X experiment interactions,

*p<.05, **p<.01.
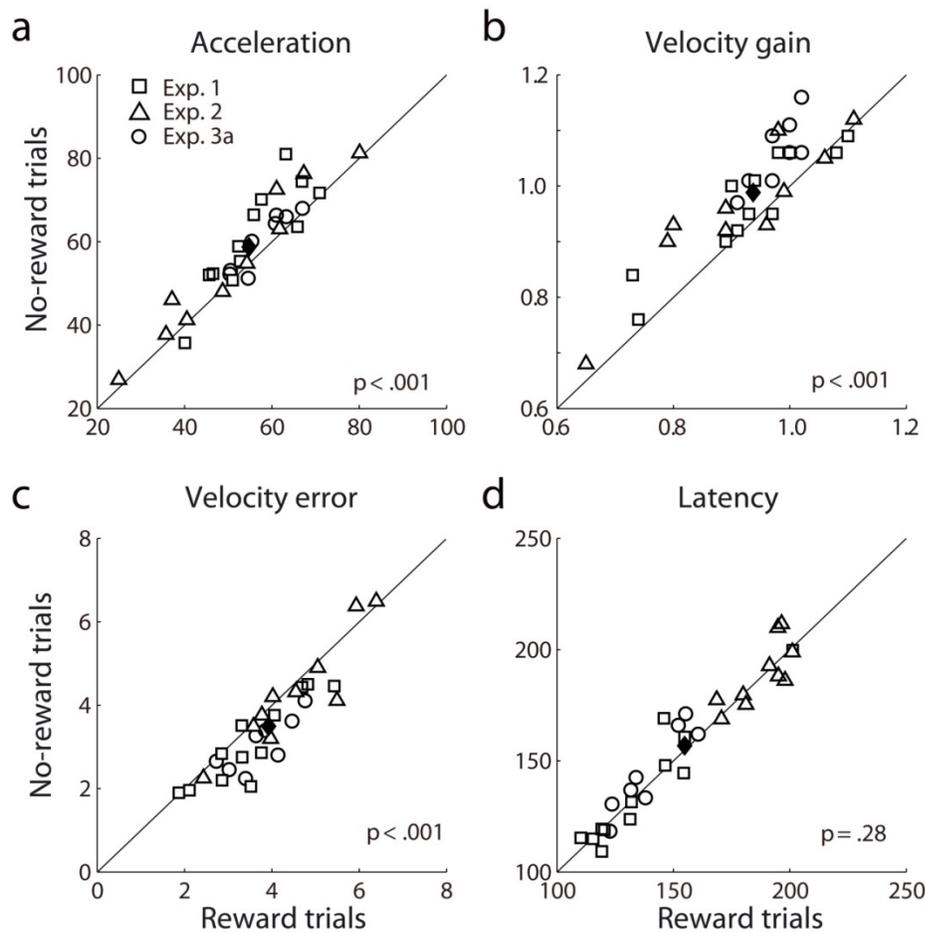
Figure 5. Mean pursuit parameters in reward vs. no-reward trials in experiments 1-3a. Each data point represents one observer; squares show results in experiment 1, triangles in experiment 2, circles in experiment 3a; filled diamonds denote means across experiments. Diagonals represent the line on which all data points would lie if means were equal across reward conditions. **(a)** Acceleration (deg/s^2). **(b)** Velocity gain. **(c)** Velocity error (deg). **(d)** Latency (ms). P-values represent significant deviations of reward indices from zero.
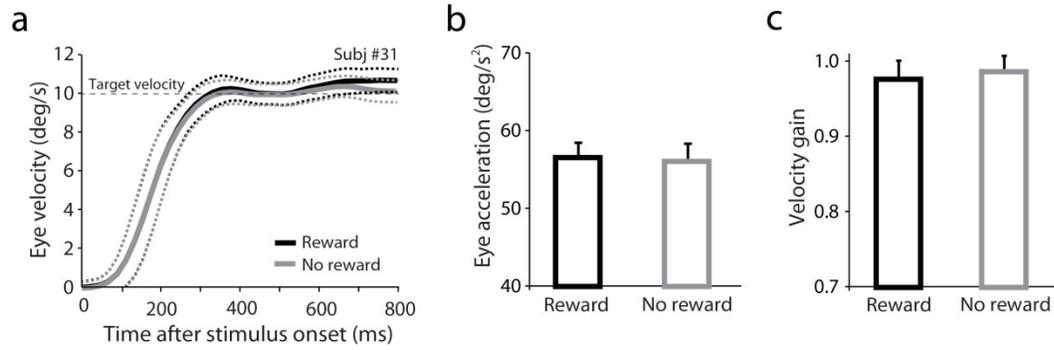
Figure 6. Reward effects in experiment 4. **(a)** Mean eye velocity traces for reward (black) and no-reward trials (gray); one representative participant. Thin lines indicate standard deviations. **(b)** Mean open-loop eye acceleration (*n*=9). **(c)** Mean closed-loop velocity gain (*n*=9). Error bars denote standard errors.