Effects of salience and reward information during saccadic decisions under risk

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Previous work has demonstrated that humans select visuomotor strategies maximizing expected gain during speeded hand movements under risk; see, e.g., [Trends Cogn. Sci. **12**, 291 (2008)]; [Glimcher *et al.*, eds., *Neuroeconomics: Decision Making and the Brain* (Elsevier, 2008), p. 95]. Here we report a similar study in which we recorded saccadic eye movements in a saccadic decision task in which monetary rewards and losses were associated with the final position of the eye movement. Saccades into a color-coded target region won points; saccades into a partially overlapping or abutting penalty region could yield a loss. The points won during the experiment were converted into a small monetary bonus at the end of the experiment. We compared participants' winnings to the score of an optimal observer maximizing expected gain that was calculated based on each participant's saccadic endpoint variability, similar to a recent model of optimal movement planning under risk [J. Opt. Soc. Am. A **20**, 1419 (2003)]; [Spatial Vis. **16**, 255 (2003)]. We used three different experimental paradigms with different interstimulus intervals (Gap, No Gap, and Overlap) to manipulate saccadic latencies and a fourth experiment (Memory) with a prolonged 500 ms delay period. Our results show that our subjects took the reward information, as specified by the different penalties, into account when making saccades and fixated onto or very close to the target region and less into the penalty region. However, the selected strategies differed significantly from optimal strategies maximizing expected gain in conditions when the magnitude of reward or penalty was changed. Furthermore, scores were notably affected by stimulus saliency. They were higher when the target region was filled and the penalty region outlined by a thin line, as compared to conditions in which the target was indicated by a less salient stimulus. Scores were particularly poor in trials with the shortest latencies (120–140 ms) mostly obtained in the Gap paradigm. At longer latencies scores improved considerably for latencies longer than 160 ms. This was in line with an improvement in accuracy for single targets up to 160 ms. Our results indicate that processing both of reward information and of stimulus saliency affect the programming of saccades, with a dominating contribution of stimulus saliency for eye movements with faster latencies. © 2009 Optical Society of America

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1. INTRODUCTION

Saccadic eye movements are a fundamental and inherent feature of human foveated vision and have been studied extensively for more than a century [1,2]. Saccadic eye movements allow us to foveate targets at different locations in the visual field in close temporal succession [3]. Saccadic eye movements have been used as an appropriate and convenient way to explore motor performance that is controlled by sensory processing; see, e.g., [4,5]. Visual information driving saccadic eye movements is processed either directly to the superior colliculus (SC) or via the primary visual cortex (V1) along the ventral stream (via V4) and the dorsal stream (via MT) toward supplementary eye fields (SEF), frontal eye fields (FEF), areas in the parietal cortex (most prominently intraparietal area LIP) and SC. Both FEF and SC are believed to play an important role in the goal selection and preparation of saccadic eye movements [6,7]. It is commonly assumed that the salience of potential saccade targets is represented in these areas. Since some of these areas are known to be affected by the processing of reward-related information, our goal here was to explore whether saccadic target selection at a fine level would also be affected by reward information and how salience and reward information is combined.

Recent years have seen a growing interest in the neural computations behind the processing of nonvisual attributes like reward, value and (monetary) gain; see, e.g., [8–11]. Neurons in LIP are believed to be responsible for the encoding of attributes like reward, (monetary) gain and value [9,12,13]. Platt and Glimcher, for instance, argue that humans and animals decide what to do in a given situation by assessing the relative value of each possible response [9]. In their experiments, different amounts of orange juice as a reward were associated with fixating one of two possible visual target locations. Neural activity in the lateral intraparietal area was found to modulate depending on the reward ratio assigned to the two target locations [9]. In a similar study, Sugrue and colleagues [13] found that neuronal activity in the parietal cortex correlates with the relative value assigned to pairs of targets. However, the authors argue that despite a trial-by-trial correlation of neuronal activity in LIP with expected reward, area LIP plays an important role in

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remapping abstract valuation to concrete action rather than directly computing attributes like reward or value [13]. Similarly, Roitman and Shadlen concluded that activity of LIP neurons is predictive for the monkey's decision in a combined motion-discrimination reaction-time task [12].

Area LIP has also been shown to increase neuronal activity in relation to saccadic eye movements in general [14] and might be involved in the allocation of spatial attention and motor intention; see, e.g., [15–17].

Besides the question of where and how reward might be coded in the brain, a separate question concerns the time course of reward information processing. Milstein and Dorris (2007) demonstrated that saccadic reaction times (SRTs) correlated negatively with relative expected value [18]. In addition, SRTs correlated more highly with relative expected value than with parameters like reward probability or reward magnitude alone. A neurophysiology study has shown that neurons in the monkey parietal cortex show increasing task-related activity with both the reward magnitude and the reward probability but do not seem to distinguish between the two components [19].

Here, we explored the fine tuning of the human saccadic system by directly linking the exact endpoint of the saccade to a reward or a loss. Our study is similar in scope to previous work concerned with reward processing during speeded hand movements under risk (see, e.g., [20,21] for review). In these speeded visuomotor decision tasks, subjects are asked to reach out and touch a computer screen within a short period of time (e.g., 700 ms). Rewards and losses are coded visually by colored circular regions on a touch monitor, and subjects can win or lose a small amount of money by touching them. Hits inside a green target region yield a small reward; accidental hits inside a nearby red penalty region incur a small loss. Movements that do not reach the screen within the time limit are heavily penalized, and following a few hundred practice trials they almost never occur. In planning movement in this task, subjects are effectively choosing among infinitely many lotteries, each associated with a particular motor strategy (see [20,22,23], for model details). To maximize the outcome of his/her hand movement, the subject should touch the green region as often as possible and avoid accidentally hitting the overlapping red penalty region, i.e., select a motor strategy that corresponds to the best trade-off between the risk of hitting the penalty region and missing the reward region. This assumption yields distinct predictions about the optimality of eye and hand movements in environments where there are explicit gains and losses associated with the outcomes of the movement and in which agents are presumed to be risk neutral. The results obtained in these studies indicate that subjects choose optimal (or almost optimal) visuomotor hand movement strategies that are well described by the predictions for an optimal decision maker maximizing expected gain ([22,24–28]). In selecting optimal movement planning strategies maximizing expected gain, subjects integrate the sensory information associated with stimulus presentation, the uncertainty due to hand movement planning, and movement execution and knowledge about the assigned rewards and penalties.

We studied the selection of eye movement strategies during *saccadic* decisions under risk. We instructed participants to rapidly make a saccade into a green target region and avoid a saccade into a nearby red penalty region. Saccadic responses into the target region won a reward (gain of 100 points per trial), and saccadic responses into the penalty region could incur a loss (loss of 500 points per trial). Scores for each participant were compared with scores of an optimal observer. Optimal scores were calculated taking into account each participant's saccadic endpoint variability, similar to a recent model of optimal (hand) movement planning under risk ([20,22,23]); see Methods, Section 2, for model details. The earlier experiments of Trommershäuser *et al.* [22,23] demonstrated that, during speeded hand movements under risk, participants selected strategies that were indistinguishable from optimal behavior maximizing expected gain.

In preparing an eye movement, several processes take place, such as shifts of visual attention to the new target, disengagement of oculomotor fixation, and computation of the kinematic movement parameters; see, e.g., [29]. There is evidence that the time needed to prepare an eye movement is modulated by the fixation task. The saccadic latency is shorter when the fixation stimulus is turned off before the onset of the target (gap paradigm) than when the fixation stimulus remains visible at target onset (overlap paradigm). This effect was reported first by Saslow [30]. The reliable finding of shorter latencies in the gap paradigm could be due to facilitation of the disengagement of fixation and attention [31,32]. Ross and Ross [31] argued that the gap effect consists of two components, a warning signal effect and a second effect that has been called fixation release or fixation disengagement. Here we asked whether saccadic eye movement planning under risk follows the same principles as hand movement planning under risk. We employed three different experimental paradigms (Gap, No Gap, and Overlap) to manipulate saccadic latencies, as well as an experiment with an increased 500 ms delay period before eye movement initiation (Memory) and compared our participants' fixation strategies with the predictions for an optimal observer maximizing expected gain.

2. METHODS

A. Equipment

Participants performed the experiments in a dimly lit room in front of a 21-in. computer monitor (ELO ET2125C, resolution 1280×960 pixels at a refresh rate of 100 Hz). A chin rest was used to control the viewing distance, which was 47 cm from the participants' eyes to the front of the screen. The experiment was programmed in C and run on a Pentium IV Dell Precision workstation. Eye movements were recorded using a head-mounted-camera-based SR-Research Eyelink II eye tracking system at a sampling rate of 250 Hz (4 ms temporal resolution).

B. Stimuli

Stimuli consisted of a target circle and a penalty circle and were presented on a gray background (luminance: 33 cd/m^2). The target and penalty circles had radii of 28 pixels (9 mm), which is equivalent to 1 deg of visual angle at this particular viewing distance. Both circles differed from the background in color and luminance. In the first of three stimulus conditions ("target filled"), the target was a filled green disk and the penalty was a thin red circle (line width 2 pixels). In the second stimulus condition ("circles"), the target was a thin green circle and the penalty was a thin red circle. In the third stimulus condition ("penalty filled"), the target was a thin green circle and the penalty was a filled red disk. The filled red circle had a luminance of 16 cd/m^2 and the filled green circle had a luminance of 67 cd/m^2.

Stimuli were presented unpredictably for the subject at a random position, within an annulus of 4°–6° (36–54 mm) eccentric from initial fixation at screen center. The two circles were presented adjacent to each other or overlapped by 0.5° (4.5 mm) (near or far spatial condition). The orientation of the stimulus configuration was chosen such that the two circles were always presented at the same distance from initial fixation within the annulus of 4°–6° (Fig. 1). The penalty circle could appear either abutting or partially overlapping the target circle and was presented at the same distance from initial fixation, shifted either clockwise or counterclockwise with respect to the target circle. The spatial position of the stimulus configuration on the screen was chosen randomly on each trial to prevent participants from relying on preplanned eye movement strategies. In 20% of the trials, only the target circle and no penalty circle was displayed (control trials, randomly interleaved).

C. Procedure

The display of a fixation cross in the screen center indicated the start of the trial. The participants were required to fixate accurately and press the y-button on a game pad, which was mounted on the table centered in front of the monitor. If fixation was not accurate within 1 deg of visual angle, an error tone was presented, and the trial had to be reinitiated.

Experiment 1 (Gap): Once the participant had pressed the button, the fixation cross was extinguished and after a gap of 200 ms the stimulus configuration was displayed.

Experiment 2 (No Gap): After the button press and a variable delay of 400–700 ms (chosen from a uniform random distribution), the stimulus configuration was presented and the fixation cross was extinguished simultaneously.

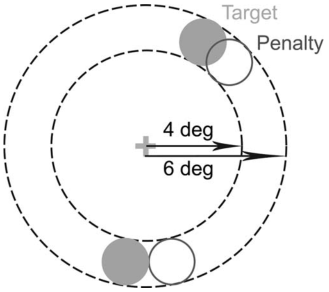

Fig. 1. Stimulus configuration. Stimuli were presented randomly within an annulus 4°–6° (36–54 mm) eccentric from initial fixation that was in the center of the screen. The circles were presented adjacent to each other or overlapped by 0.5° (4.5 mm; far or near spatial condition). The orientation of the stimulus configuration was such that the distance from initial fixation to the two circle centers was the same. The penalty circle could appear either clockwise or counterclockwise with respect to the target circle.

Experiment 3 (Overlap): After the button press and a variable delay of 400–700 ms (chosen from a uniform random distribution), the stimulus configuration was presented and the fixation cross remained visible on the screen.

Experiment 4 (Memory): After the button press and a variable delay of 400–700 ms (chosen from a uniform random distribution), the stimulus configuration was presented for 100 ms while the fixation cross remained visible. After a delay of 500 ms the fixation cross was extinguished and the participants had to make a saccade to the remembered location of the stimulus configuration. An error tone was presented and the trial was discarded if the participant made a saccade before the fixation cross was extinguished. See Fig. 2 for an illustration of all 4 experiments.

Participants received feedback about their saccadic end position after each trial as follows: If the participant's first saccade landed within the area of the circles, the circle that was "hit" (or both, if both were hit) "exploded" graphically. Then, the points awarded for that trial were shown, followed by the participant's total accumulated points for that session. Besides feedback about whether the saccade had hit inside the target or penalty region (or both), participants did not receive further spatial feedback about their saccadic end point. A saccade into the target circle gained 100 points. The penalty for making a saccade into the penalty circle was constant within a block and could amount to a loss of 0 or 500 points. If the first saccade landed in the region where target and penalty circles overlapped, participants incurred the reward and the loss. If the participants' saccades landed neither in the target nor in the penalty circle, no reward or loss was issued. The value associated with the penalty region alternated between 0 and 500 points across 16 blocks (penalty value 0 in blocks 1–4 and 9–12, penalty value 500 in blocks 5–8 and 13–16). Each block consisted of 40 trials. In 58% of the trials, more than one saccade was detected. These corrective saccades landed almost always in the target zone and were not analyzed further as they did not contribute additional information for the purposes of the study.

A single condition consisted of at least 12 warm-up trials and 16 blocks of 40 trials each. Each block of trials consisted of eight repetitions of each of the 4 spatial stimulus configurations and 8 control trials, presented in random order. Participants needed approximately 60–70 min to complete each condition. Participants repeated the calibration of the eye tracking system every 120 trials to ensure high calibration accuracy throughout the experiment (averaged spatial saccadic error ~0.2°/18 mm). (The calibration error of 0.2° (1.8 mm) corresponds to an average mean deviation of 0.033° (0.3 mm) for the recorded mean saccadic endpoints and of 5 points for the measured gains, estimate computed based on 36 calibration trials.) We did not constrain our subjects' eye movements by a specific time limit but instructed them to look at the target as quickly and accurately as possible and win as many points as possible.

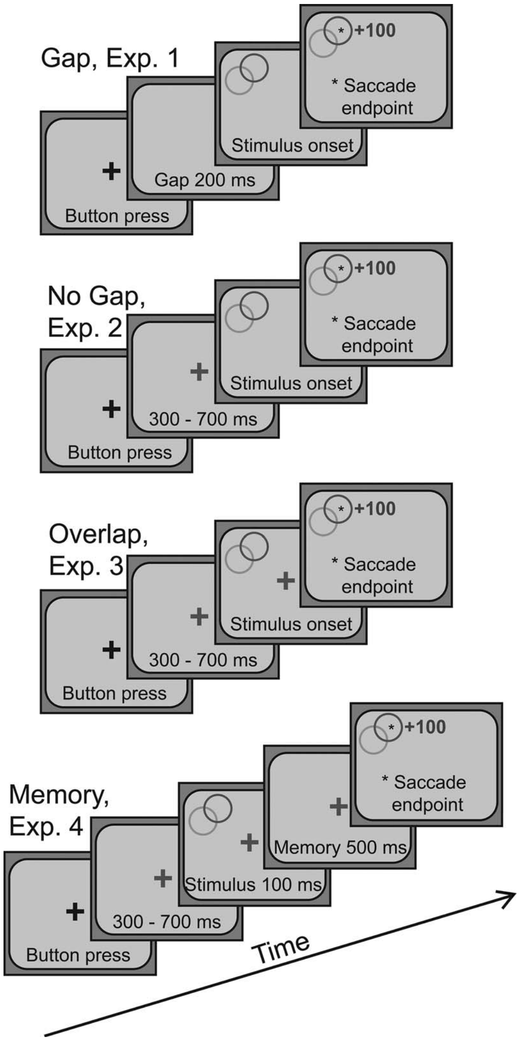

Fig. 2. Trial procedure. The display of a fixation cross at screen center indicated the start of the trial in all four experiments. The participant was required to fixate accurately and then press a button. A saccade into the target circle gained 100 points. The penalty for making a saccade into the penalty circle was constant within a block and could amount to a loss of 0 or 500 points. If the first saccade ended in the region where target and penalty circles overlapped, the reward and penalty were combined; if the participants' saccade landed in neither of the circles, no reward or loss was issued.

Data collection was carried out over several sessions conducted on different days. The order of conditions within an experiment was randomized across participants.

D. Participants

Six participants participated in this study; all six took part in experiment 1, and all except KB and NH took part in experiments 2, 3, and 4. The participants were five female psychology undergraduate students of the University of Giessen and the first author. All participants had normal or corrected-to-normal vision and ranged from 22 to 32 years in age. All participants except the first author were naïve with respect to the hypotheses under test. Participants were informed of the payoffs and penalties for each block of trials. Written, informed consent was obtained from the participants prior to their inclusion in the study, and the rights of the participants were protected according to the 1964 Declaration of Helsinki. Participants were paid 8 € per hour for their participation in the experiment.

Participants were also informed about their current cumulative score after each trial and competed for the overall high score in each experiment. The points won by the participants were converted into a monetary bonus; i.e. participants earned 0.50 € per every 5,000 points in addition to the fixed amount of 8 € per hour.

E. Data Analysis

In each trial, we recorded eye position and thus saccadic reaction times (i.e., the time between the go signal and the onset of the first saccade), saccadic endpoints, and score. To allow for a direct comparison across spatial conditions, all configurations were aligned along the same orientation, defining an x direction subtending target center and penalty center and a y direction perpendicular to x. For each participant, the mean distance in the x direction between the target center and the final saccadic position (mean saccadic endpoint) and variability of the saccadic endpoints were calculated individually.

Eye movements were recorded using a head-mounted-camera-based SR-Research Eyelink II eye tracking system at a sampling rate of 250 Hz (4 ms temporal resolution). The standard Eyelink II criterion was used for saccade detection. The Eyelink eye tracker uses an automatic saccadic detection algorithm based on a velocity threshold of 35 deg/s and an acceleration threshold of 9500 deg/s^2 (using the Euclidean sum of horizontal and vertical angles). Velocity is computed based on two samples, acceleration based on a weighted sum of three samples. The saccade detector becomes active if either the velocity or the acceleration exceeds threshold. A saccade is defined as a period when the saccade detector is active for two or more samples in sequence and continues until the saccade detector is inactive for at least five samples. The saccadic endpoint positions generated by the Eyelink II software were used to assign the feedback, displayed at the end of each trial. The remaining data analysis was conducted offline using Matlab routines; statistical computations were done using SPSS. Trials in which the saccadic reaction time of the participant was shorter than 80 ms were considered anticipatory and excluded from analysis. Each participant contributed at least 600 data points per experiment in experiments 1, 2, and 3 (300 data points in experiment 4); i.e., 120 (60) repetitions per spatial condition (near and far) and penalty value (0 and 500) as well as 120 (60) control trials. All in all, 16% of the raw data was excluded from data analysis.

Saccadic endpoints were analyzed with respect to endpoint variability and relative distance in the x direction from the target center. Trials were sorted by saccadic latency in ascending order and divided into sextiles (quantiles of six equal proportions).

F. Optimality of Saccadic Eye Movements under Risk

We compared each participant's performance with the performance of an optimal eye movement planner maximizing expected gain, similar to a recently proposed model of optimal hand movement planning under risk [22,23]. According to our model, an optimal visuomotor movement strategy is defined as the eye movement strategy that maximizes the subject's expected gain [20,33].

The model takes into account the explicit gains associated with the possible outcomes of the eye movement and the participant's own task-relevant saccadic endpoint variability. For the conditions of our experiment, the expected gain $\Gamma(S)$ of visuomotor strategy S is defined by

$$\Gamma(S) = \sum_{i=1}^{2} G_i P(R_i|S), \tag{1}$$

where $P(R_i|S)$ is the probability given a particular choice of strategy S, and G_i is the gain associated with a saccadic response into region R_i of making a saccade into the target region R_1 or the penalty region R_2. In this model, the visuomotor strategy S is identified with the mean saccadic endpoint on the screen $(\bar{x},\bar{y})$. We found that saccadic endpoints were distributed around the mean saccadic endpoint $(\bar{x},\bar{y})$ according to a bivariate Gaussian distribution (widths σ_x and σ_y),

$$p(x,y|\bar{x},\bar{y},\sigma_x,\sigma_y) = \frac{1}{2\pi\sigma_x\sigma_y} \exp[-(x-\bar{x})^2/2\sigma_x{}^2] \times \exp[-(y-\bar{y})^2/2\sigma_y{}^2]. \tag{2}$$

Once participants were practiced in the task, variability in the y direction (direction of the saccade) was slightly higher than variability in the x direction (as typically found in similar tasks; see, e.g., [34,35]) and remained constant throughout the experiment (i.e., independent of spatial and penalty conditions). Thus, under these conditions the probability of hitting region R_i is then defined by the choice of $(\bar{x},\bar{y})$ on the screen and the participant's endpoint variability $\sigma=(\sigma_x,\sigma_y)$ as

$$P(R_i|\bar{x},\bar{y},\sigma_x,\sigma_y) = \int_{\mathrm{d}x}\int_{\mathrm{d}y} p(x,y|\bar{x},\bar{y},\sigma_x,\sigma_y)\mathrm{d}x\mathrm{d}y. \tag{3}$$

Under these assumptions, the optimal eye movement strategy corresponds to the mean saccadic endpoint $(\bar{x}_{\mathrm{MEG}},\bar{y}_{\mathrm{MEG}})$ on the screen maximizing Eq. (4),

$$\Gamma(\bar{x},\bar{y}) = \sum_{i=1}^{2} G_i P(R_i|\bar{x},\bar{y},\sigma_x,\sigma_y). \tag{4}$$

In our experiment, this maximum expected gain strategy $(\bar{x}_{MEG},\bar{y}_{MEG})$ varies with the position and magnitude of the penalty. When the penalty is zero, the optimal mean endpoint position is the center of the target region. For nonzero penalties, the optimal mean saccadic endpoint shifts away from the penalty region and, therefore, away from the center of the target. This shift is larger for greater penalties, for penalty regions closer to the target, and for participants with greater saccadic endpoint variability σ.

Note that the model uses measured saccadic endpoint variability as an estimate for each participant's saccadic variability and yields predictions for optimal performance that maximizes expected gain depending on saccadic endpoint variability, target and penalty value, and target size and position (for more model details see also [22,23,27]). We estimated each participant's saccadic endpoint variability from the distribution of saccadic endpoints in the control trials (presentation of target circle only) for each experiment. Saccadic endpoint variability did not differ significantly for the three saliency conditions in the control trials [endpoint variability in the x direction: Bartlett test, $\mathrm{F}_{(2,2008)}=0.9663$, $\mathrm{p}=0.38$; endpoint variability in the y direction, Bartlett test, $\mathrm{F}_{(2,2008)}=2.4435$, $\mathrm{p}=0.09$; average endpoint variability estimates pooled across six subjects and the x and y directions in the Gap condition: $\sigma_{\text{target filled,6VPs}}=0.78°$ (7.0 mm), $\sigma_{\text{both hollow,6VPs}}=0.79°$ (7.08 mm), $\sigma_{\text{target filled,6VPs}}=0.80°$ (7.23 mm)]. Thus, we computed averaged variability estimates across the three saliency conditions. Note that this variance in the measurements of the distributions also includes eye-tracker noise and a small calibration error $<0.2°$ (1.8 mm).

To get an estimate of the minimum time needed for the processing of reward information, we compared the fastest latencies with the latencies at which performance reached optimal performance. We estimated the fastest response times by estimating the value of the (lowest) 5th percentile of the latency distribution in each condition. Performance was classified as optimal based on a comparison with the 95% confidence interval of optimal performance maximizing expected gain (see next paragraph for details on the computations of model predictions).

G. Comparison of Model Predictions and Behavioral Results

For the model predictions, we computed separate estimates of variability in the x direction and the y direction for each participant and each experiment from the control trials in which only the target circle was displayed. Saccadic endpoint variability differed significantly among the individual subjects but remained largely constant across the four experiments and in the x and y directions [average variability estimates, pooled across six (Gap) or four (No Gap, Overlap, Memory) subjects: $\sigma_{\text{Gap,6VPs}}=0.42°$ (3.78 mm); $\sigma_{\text{No Gap,4VPs}}=0.37°$ (3.29 mm); $\sigma_{\text{Overlap,4VPs}}=0.48°$ (4.36 mm); $\sigma_{\text{Memory,4VPs}}=0.75°$ (6.78 mm)]. We therefore compared the behavioral results with the model predictions based on individual average variability estimates per subject.

We classified behavior as being significantly suboptimal if it fell outside the 95% confidence interval of optimal performance as predicted by Eq. (4). For each subject and condition, we computed 95% confidence intervals of optimal performance by performing Monte Carlo simulations of the respective number of trials in each condition, based on the measured mean saccadic endpoint and endpoint variance.

3. RESULTS

A. Distribution of Saccadic Endpoints and Saccadic Latency

Trials were sorted by saccadic latency and divided into sextiles for analyses. Figure 3 shows the typical distribution of saccadic endpoints of the fastest and the slowest sextiles of all experiments. Saccades with the shortest latencies in the Gap experiment exhibited an undershoot of about 1° (9 mm) and clustered around the vertical symmetry axis of the target / penalty configuration. Saccades with the longest latencies in the Gap experiment did not undershoot and ended close to the target center. In the No Gap experiment, saccades with the shortest latencies exhibited only a tiny undershoot and landed close to the target center, slightly biased into the direction of the penalty region. Saccades with longer latencies in the No Gap experiment did not exhibit this bias and ended in the center region of the target. In the Overlap experiment, saccades landed in the center region of the target, whereas in the Memory experiment, saccades clustered around the vertical symmetry axis of the target but undershot the center of the circle by an amount of 0.75° (6.75 mm). Surprisingly, this undershoot increased with longer latencies (Fig. 3). To investigate the effects of spatial condition (near versus far) and penalty value (penalty 0 versus penalty 500) on the shift of the mean saccadic endpoint away from the penalty region, we conducted a three-way ANOVA with the factors experiment, spatial condition, and penalty value, individually for all participants. The results of our analysis showed a significant difference in experiments on the distribution of saccadic end points ($p<0.001$ for all participants) and also a significant difference in shifts of saccadic endpoints for the near and far conditions for all participants [$F(1,5309)=18.1$, $p<0.001$; $F(1,5739)=6.92$, $p<0.01$; $F(1,5739)=17.3$, $p<0.001$; $F(1,5958)=62.6$, $p<0.001$]. We observed a significant main effect of penalty value on shift of saccadic endpoints for three out of four participants [$F(1,5309)=13.6$, $p<0.001$; $F(1,5739)=0.61$, $p=0.44$; $F(1,5739)=5.3$, $p<0.05$; $F(1,5958)=14.6$, $p<0.001$]. However, in all experiments, the shift of the mean saccadic endpoint from the target center was much smaller than predicted for an optimal eye movement planner maximizing expected gain [as defined by Eq. (4)]. There was no significant interaction of spatial condition and penalty value.

As expected, the range of saccadic latencies differed significantly across experimental paradigms Gap, No Gap, Overlap, and Memory for all participants [ANOVA $F(3,6667)=1059$, $p<0.001$; ANOVA $F(3,7183)=2921$, $p<0.001$; ANOVA $F(3,7194)=432$, $p<0.001$; ANOVA $F(3,7440)=1198$, $p<0.001$].

B. Hits, Score, and Distance to the Target

For latencies >160 ms, saccadic accuracy remained largely constant for both conditions in which target and penalty circle were overlapping (near condition) and when they were abutting (far condition) (Fig. 4). Across all conditions and experiments, subjects fixated close to the center of the green target, even if this behavior corresponded to grossly suboptimal eye movement strategies, and resulted in largely negative scores due to frequent accidental fixations into the penalty region.

In the Gap experiment, subjects fixated closer to the target center in trials with longer latencies as compared with trials with shorter latencies. The distance between saccadic endpoint and target center decreased on average from about 1.2° (11 mm) in the Gap experiment for trials with the shortest latencies to about 0.89° (8 mm) for trials with the longest latencies. This effect was mostly absent

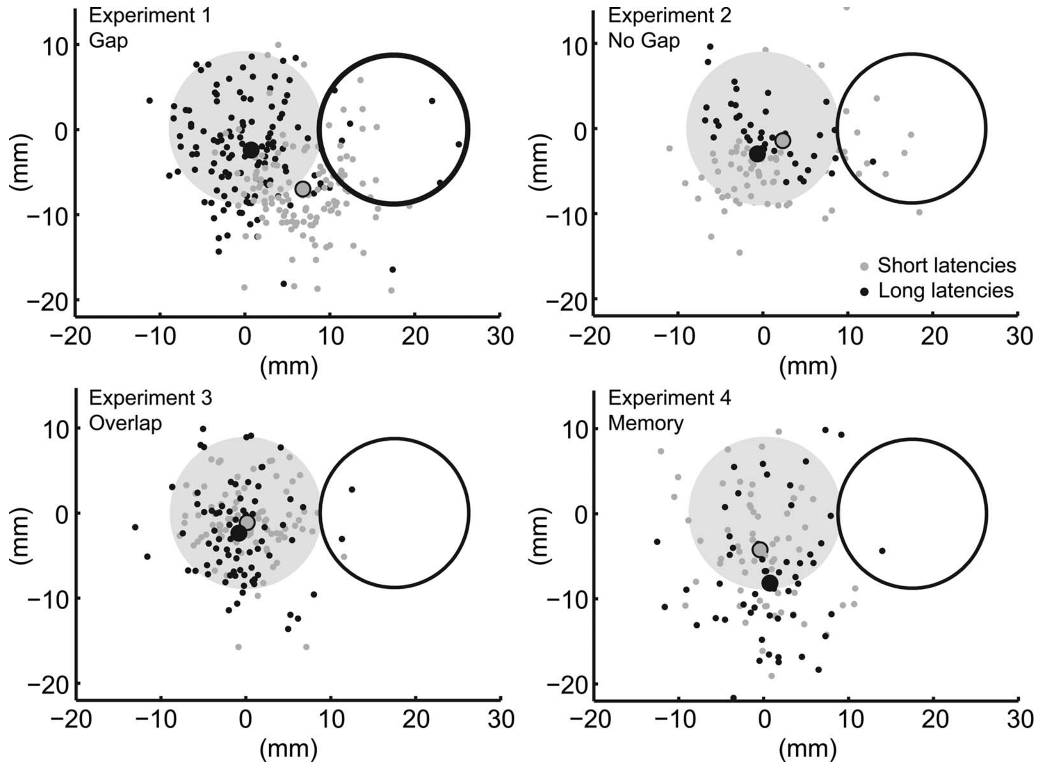

Fig. 3. Typical distribution of saccadic endpoints. Data pooled across participants, far spatial configuration, target filled, penalty 500 points. Trials were sorted by latency and grouped into sextiles. The gray dots indicate saccadic endpoints from the sextile with shortest latencies; the black dots indicate saccadic endpoints from the sextile with longest latencies. Circles denote the mean of a sextile. The large gray circle denotes the target area; the hollow black circle denotes the penalty area. Upper left panel, data from experiment 1 (Gap); upper right panel, data from experiment 2 (No Gap); lower left panel, data from experiment 3 (Overlap); Lower right panel, data from experiment 4 (Memory).

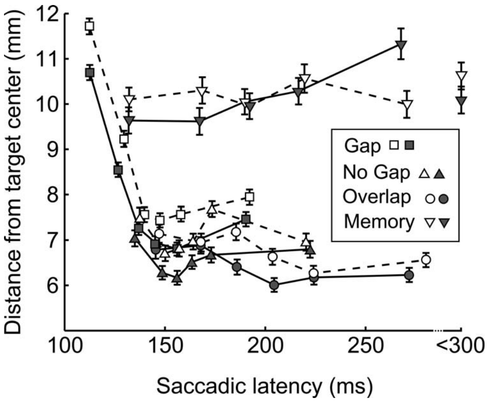

Fig. 4. Endpoint distance to target center. Distance between mean saccadic endpoints and the target center as a function of saccadic latency. Data were grouped into sextiles. Different symbols denote different experiments; the solid lines/gray symbols show data from the far spatial condition; the dashed lines/open symbols show data from the near spatial condition. Data pooled across participants, penalty conditions, and saliency conditions. Error bars denote ±1 SEM.

in the other three experiments. In the No Gap experiment, the distance decreased from about 0.83° (7.5 mm) for trials with the shortest latencies to about 0.78° (7 mm) for trials with the longest latencies. In the Overlap experiment, the distance decreased from about 0.78° (7 mm) to about 0.67° (6 mm). In the Memory experiment, the distance between mean saccadic endpoint and the target center remained constant at about 1.1° (10 mm) on average (all estimates were computed by averaging across all participants, penalty, and luminance conditions).

The shift in mean saccadic endpoint differed significantly for the two spatial stimulus configurations but not across the two penalty conditions. This result is mostly due to the lack of effect in the near condition. A three-way ANOVA with the factors experiment, spatial condition, and penalty value yielded a significant main effect of spatial condition on distance to the target center in three out of four participants [$F(1,5309)=0.14$, $p=0.71$; $F(1,5739)=6.73$, $p<0.01$; $F(1,5739)=18.4$, $p<0.001$; $F(1,5958)=52.2$, $p<0.001$], but no effect for penalty value ($p>0.05$ for all participants). Subjects in general fixated closer to the target center with longer latencies (see also below and Fig. 7 below), for both the near and far condition.

As a direct consequence of the mean of the distribution of saccadic endpoints being dependent on saccadic latency, the percentage of hits into the target region, the penalty region, and the background also varied with saccadic latency. As shown in Fig. 5, the percentage of hits into the background in the Gap experiment for trials with short latencies was as high as 60%, and hit percentage into the target region was about 30%. At latency levels of 150 ms and above, hit percentage into the background stabilized at about 30% and hit percentage into the target region reached about 70%. The percentage of hits into the penalty region decreased slightly for longer saccadic latencies. In the Gap, No Gap, and Overlap experiments, a small effect of stimulus saliency (target filled versus circles versus penalty filled) was observed (see also Fig. 5). The percentage of hits into the target region in fast trials was significantly lower than the percentage of hits in slow trials for three out of four participants in the Gap experiment (χ^2-test: $\chi^2_1=136.4$, $p<0.001$; $\chi^2_1=18.2$, $p<0.001$; $\chi^2_1=0.93$, $p=0.34$; $\chi^2_1=46.2$, $p<0.001$), in the No Gap experiment (χ^2-test: $\chi^2_1=9.05$, $p<0.01$; $\chi^2_1=0.39$, $p=0.53$; $\chi^2_1=17.6$, $p<0.001$; $\chi^2_1=17.8$, $p<0.001$) and in the Overlap experiment ($\chi 2$-test: $\chi^2_1=8.76$, $p<0.01$; $\chi^2_1=0.69$, $p=0.41$; $\chi^2_1=27.6$, $p<0.001$; $\chi^2_1=30.0$, $p<0.001$). This was not the case in the Memory experiment ($\chi 2$ test: $p>0.05$ for all participants). All participants reached higher scores when the target circle was filled compared to when the penalty circle was filled in the 'Gap' experiment (χ^2-test: $\chi^2_3=7.65$, $p=0.05$; $\chi^2_3=4.60$, $p=0.20$; χ^2-test: $\chi^2_3=62.5$, $p<0.001$; χ^2-test: $\chi^2_3=15.4$, $p<0.01$) and in the No Gap experiment (χ^2-test: $\chi^2_3=12.5$, $p<0.01$; χ^2-test: $\chi^2_3=5.91$, $p=0.12$; χ^2-test: $\chi^2_3=100.6$, $p<0.001$; χ^2-test: $\chi^2_3=12.3$, $p<0.01$). The same effect was found in the Overlap and Memory experiments. All participants except participant 3 reached higher scores when the target circle was filled in the Overlap experiment (χ^2-test: $\chi^2_3=6.98$, $p=0.07$; χ^2-test: $\chi^2_3=83.9$, $p<0.001$; χ^2-test: $\chi^2_3=6.89$, $p=0.07$) and in the Memory experiment (χ^2-test: $\chi^2_3=51.3$, $p<0.001$; χ^2-test: $\chi^2_3=118.6$, $p<0.001$; χ^2-test: $\chi^2_3=9.77$, $p<0.05$), even though the difference did not always reach significance.

C. Optimality of Saccadic Eye Movements Under Risk

As shown in Fig. 6, performance improved with longer saccadic latencies in the Gap, No Gap, and Overlap experiments and remained largely constant in the Memory experiment. Figure 6 compares observed and optimal efficiencies (actual scores divided by optimal scores for the eye movement planner maximizing expected gain) for penalty 0 and penalty 500 conditions as a function of saccadic latency. Overall, performance consistently failed to reach optimal performance, ranging between 80% and 100% of optimal performance maximizing expected gain in the Gap, No Gap, and Overlap experiments (data pooled across participants and spatial conditions; Fig. 6). Saccades with the shortest latencies in the Gap experiment mark an exception here, with performance reaching only about 40%–55% of optimal performance maximizing expected gain. In the Memory experiment, performance reached about 80% of optimal performance maximizing expected gain and did not covary with saccadic latency. In penalty 500 trials, participants reached 50% optimality in the Gap experiment, 70% optimality in the No Gap, experiment and 85% optimality in the Overlap experiment. Overall, optimal performance was reached, i.e., fell into the 95% confidence interval of optimal performance, in 52 out of 216 conditions.

We compared our participants' performance with optimal performance maximizing expected gain for each subject and condition individually, based on a comparison with the 95% confidence intervals indicating the range of optimal performance, computed based on measured saccadic mean and endpoint variance in this condition (see also Subsection 2.F: Optimality of Saccadic Eye Movements under Risk); the total of 216 conditions refer to the 6 participants in three saliency conditions, two penalty conditions, and two spatial conditions in the Gap experi-

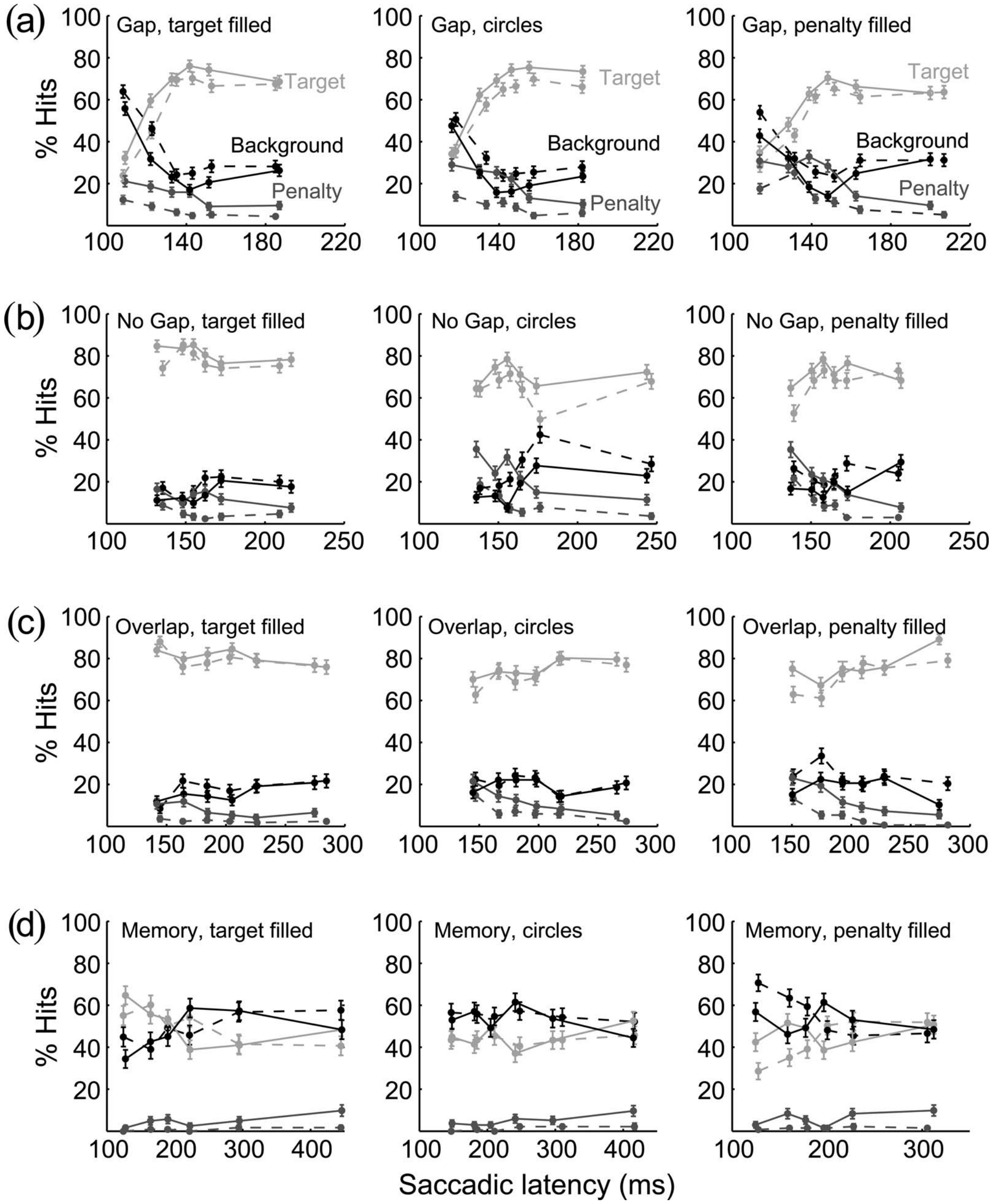

Fig. 5. Target and penalty hit frequency. Percentage of hits into the target (gray circle symbols), penalty (gray squares) and background area (black circle symbols) as a function of saccadic latency for three saliency conditions (left panels, target filled; center panels, circles; right panels, penalty filled). Data were pooled across participants and penalty conditions and grouped into sextiles. The solid lines indicate data from the near spatial condition, the dashed lines indicate data from the far spatial condition. (a) Gap experiment, (b) No Gap experiment, (c) Overlap experiment, (d) Memory experiment. Error bars denote ±1 SEM. Please note the difference in scaling of the *x* axis.

ment, and four participants in three saliency conditions, two penalty conditions, and two spatial conditions in the No Gap, Overlap, and Memory experiment.)

Optimal performance was reached mostly in the experiments with slower latencies, indicating that a prolonged preparatory period facilitated optimal or near-optimal performance (Overlap: optimality reached in 19 out of 48 conditions; Memory: 19 out of 48 conditions with optimal performance, Gap: 9 out of 72 conditions with optimal performance; No Gap: 5 out of 48 conditions with optimal performance). Moreover, optimal performance maximizing expected gain occurred more frequently in penalty 0 conditions (36 versus 16 in penalty 500 trials) and when the target circle was filled (26 versus 15 in the circle conditions and 11 in the penalty filled conditions).

The optimal eye movement strategy maximizing expected gain predicts a horizontal shift from the target center in the opposite direction from the penalty region. This predicted optimal shift is larger for stimulus conditions in which target and penalty region are closer, i.e., in the near as compared to the far condition. We found that, overall, subjects chose eye movement strategies that deviated from the predictions for the optimal eye movement planner maximizing expected gain and consistently failed to direct their gaze sufficiently far away from the target center and thus either fixated near the target center or

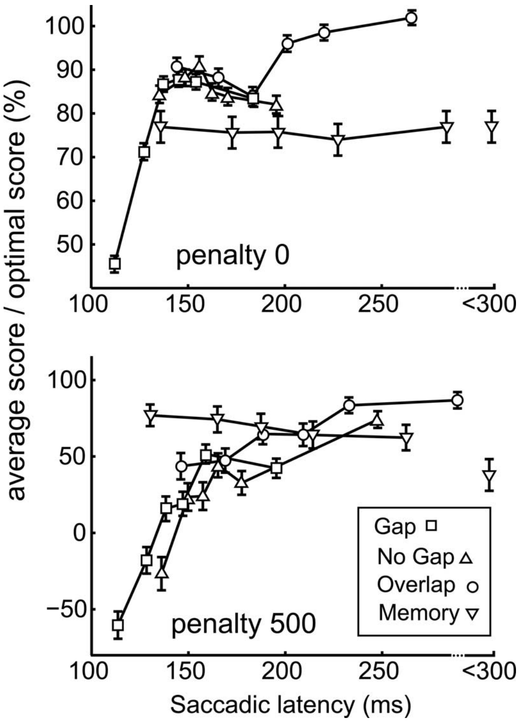

Fig. 6. Comparison of normalized average score across experiments as function of saccadic latency. Comparison of efficiency (actual scores divided by optimal scores) for penalty 0 and penalty 500 conditions as a function of saccadic latency. Data were grouped into sextiles. Different symbols denote different experiments. Upper panel, penalty 0 condition; lower panel, penalty 500 condition. Data pooled across participants, spatial conditions, and saliency conditions. Error bars denote ±1 SEM. Please note the difference in scaling of the *y* axis.

even into the penalty region in the conditions in which target and penalty region overlapped (near condition). This resulted in grossly suboptimal strategies (Figs. 6 and 7).

We finally compared the conditions in which our participants' scores reached optimal performance maximizing expected gain with those in which they did not. We compared performance at saccadic latencies at which optimal performance was first reached with performance measured at the 5th percentile of the latency distribution (to get an estimate for performance at these fastest response times). Responses from the Memory experiment in general showed a larger range of saccadic latencies, whereas performance in the other three experiments was more consistent. The average difference between the percentile of latencies at which performance fell into the range of the 95% confidence interval of optimal performance was first reached and the latency value at the 5th percentile was 35 ms (estimate computed by pooling across all conditions and participants for those conditions in which performance reached optimal performance). This indicates that, compared with the (express) saccades executed with the fastest latencies, participants needed an additional 35 ms to accurately fixate the target and to discriminate between target and penalty region.

D. Comparison Across Experiments

In the Memory experiment, the distribution of saccadic endpoints did not covary with saccadic latency. Accordingly, the frequency of hits into the target and penalty circle, the distance from the saccadic endpoint to the target center, and performance did not depend on saccadic latency either. In the other three experiments, especially the Gap experiment, participants' performance did depend on saccadic latency. Interestingly, scores for a specific given latency were very similar in all three experimental paradigms. For instance, scores within the latency range of 160–200 ms did not differ significantly when compared across experiments. This was the case for penalty 0 trials (χ^2-test: $p > 0.05$ for all participants) and penalty 500 trials (χ^2-test: $p > 0.05$ for all participants, see also Fig. 6).

4. DISCUSSION

In a series of four experiments, we studied contributions of top-down reward information and bottom-up salience during saccadic eye movements under risk. Our participants made saccadic eye movements to pairs of stimuli presented at 4°–6° eccentricity. Saccades that ended inside the target region incurred a reward; saccades that ended inside the penalty region incurred a loss. Across four experiments we manipulated saccadic latencies by varying the time interval between initial fixation and stimulus presentation. Participants' performance, i.e., the percentage of hits into the target region and the overall score, increased systematically with longer latencies of the saccadic response. Saccadic latencies at which optimal performance was reached were on average 35 ms slower than the fastest (suboptimal express) saccadic latencies at the level of the 5th percentile of the latency distribution. We did not give our subjects a time constraint for initiating or executing their eye movements but instructed them to look at the target as accurately as possible. Saccade planning in general benefitted from longer processing times preceding eye movement initiation. Higher visual saliency of the target region facilitated saccadic endpoints into the target region; this resulted in higher scores in these conditions, especially in the conditions of lowest penalty value.

Performance in trials with a 200 ms gap period covaried with saccadic latency similarly to performance in trials without a gap period. This suggests that motor processes such as disengaging fixation and attentional processes of target selection can occur in parallel. In the Memory experiment, subjects waited an additional 500 ms delay period before initiating their eye movement. Performance in general was high in this condition and did not vary with saccadic latency. The conditions of the memory-guided task were different insofar as participants were required to wait 500 ms before initiating their saccade. Our results indicate that this time window of 500 ms provides enough time to form a well-formed saccade plan (see also [36,37]).

A. Saccades versus Pointing

We next discuss the differences in performance found for rapid pointing under risk and the saccadic strategies observed in our task. The visuomotor strategies selected during rapid hand movements under risk are typically indistinguishable from or very close to optimal performance

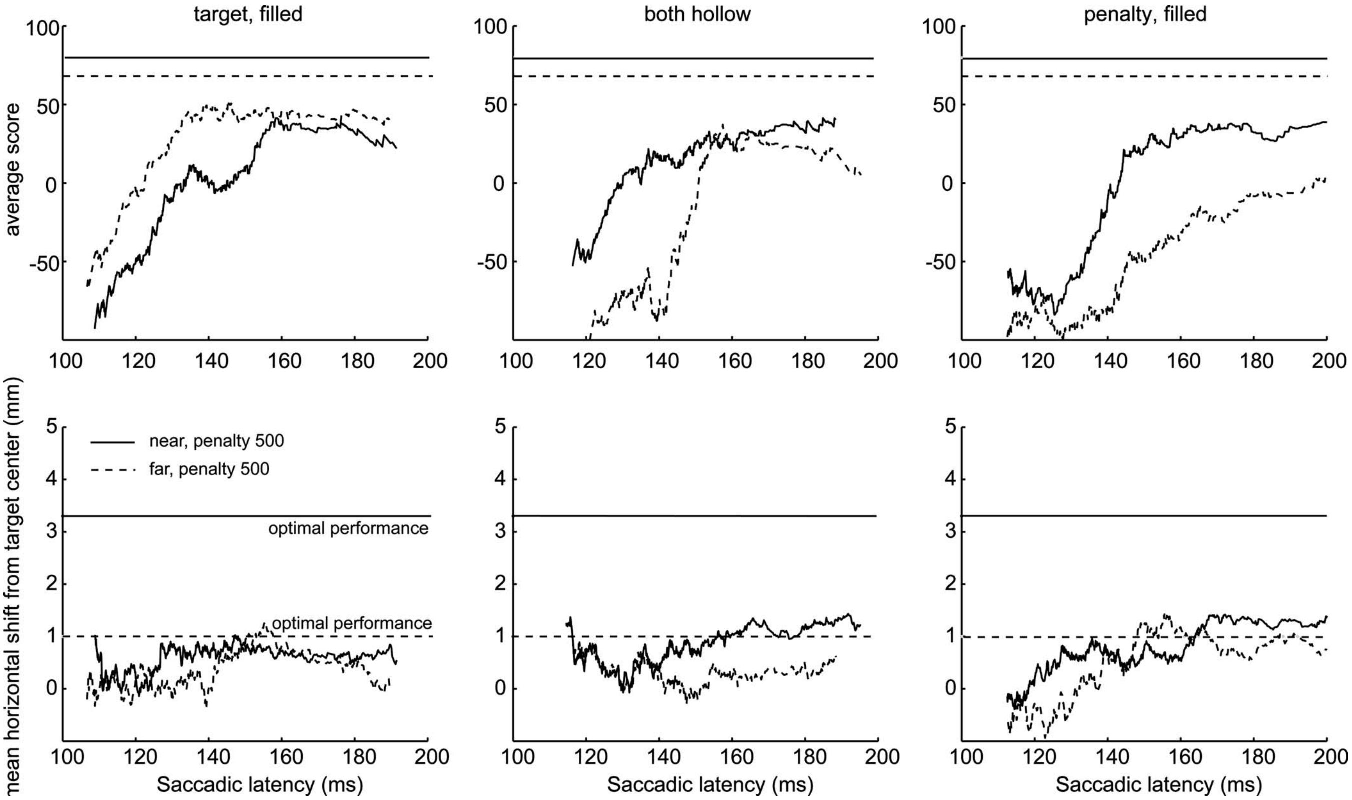

Fig. 7. Comparison of behavioral results with the predictions for the optimal eye movement planner. Upper panel, comparison of average scores as function of saccadic latency (penalty 500 condition, near and far condition, gap condition); lower panel, comparison of shift in mean saccadic end point in horizontal direction as function of saccadic latency (penalty 500 condition, near and far condition, gap condition). Data pooled across six participants, shown separately for the three saliency conditions; model predictions computed based on pooled, averaged variability estimates (pooled across six subjects).

maximizing expected gain [22–25] and reach higher efficiencies than the saccadic strategies observed in our task. One apparent difference between pointing and saccadic movement concerns the feedback available after movement initiation. Once a pointing movement is initiated, there is still plenty of time for visual feedback to be used to correct the hand movement (e.g., [38]) and to generate an estimate about the expected movement error associated with movement completion [25]. Visual feedback during the movement allows for movement corrections and enhances motor performance [39]. Accordingly, eye movements recorded during natural movement tasks (e.g., ice hockey or cricket) suggest that visual information is gathered as quickly as possible by fast and very accurate eye movements to ensure the highest possible performance, e.g., [40,41]. Furthermore, in real life there is usually no direct or costly consequence for a slightly incorrect eye movement, whereas in pointing or reaching there often is. Incorrectly pointing or reaching out for an object can thus lead to very different consequences than a slightly misfocused eye movement. One might hit an obstacle while reaching for something or knock over a glass of wine that is standing on the table.

Eye movements during hand movements typically simply seem to serve the purpose of bringing the target into focus. If the first saccade ends not exactly on the desired spot, a second, corrective saccade is made to finally align target and fovea. This happens very rapidly and usually without any disadvantages for the performance in a natural task, which also due to the fact that eye movements are usually faster than pointing movements; see, e.g., [42,43]. In addition, it has been shown that making a saccade can be rather economic and preferable compared with fully utilizing visual short-time memory capacity in a visual short-term memory task [44], which could be regarded as an indicator that making a saccade is relatively "cheap" and requires only little effort.

B. Contribution of Bottom-Up and Top-Down Factors

There is evidence from a number of studies that the target selection of saccadic eye movements is heavily influenced by bottom-up features like visual saliency (color, contrast, orientation) of the stimulus [45,46] or the luminance-defined center of gravity of a stimulus configuration, e.g., [47,48]. However, recent studies have argued that saliency cannot fully account for all aspects of human gaze behavior [49] and have emphasized the importance of the task at hand as a crucial determinant, e.g., [50,51]. Additional evidence that both bottom-up and top-down features influence the execution of saccadic eye movements comes from a study that investigated eye movements during the above-described speeded pointing tasks under risk [27]. In this study by Stritzke and Trommershäuser, participants had to point to a color-coded target region on a screen while trying to avoid an adjacent penalty region. Saccades were initially directed toward the visually more salient part of the stimulus configuration regardless of whether this salient part of the stimulus was the target or the penalty region. Later during the pointing movement, a second saccade was performed away from the salient part of the stimulus configuration toward the finger endpoint.

The results of our study can be explained by two parallel processes: (1) stimulus localization, i.e., rapid processing of stimulus features like color/contrast/shape with peripheral vision, and (2) computing and targeting the optimal endpoint based on computing (maximum) expected gain. If—in the trials with short latencies—a saccade is quickly planned without complete processing of color/reward information, it is too late to update this information once the eye movement has been initiated. Under these conditions saccadic endpoints are mainly influenced by low-level features such as the luminance-defined center of gravity [47,48] or visual saliency of the stimulus [45]. The contribution of low- level features, however, is modulated by saccadic latency. Several studies have pointed out the importance of the specific task for saccadic behavior, e.g., [50,51]. In agreement with these results, we argue that in trials with longer latencies, task-related features like the intention to hit the target and the analysis of reward related information carry more weight than bottom-up stimulus features and therefore performance increases with saccadic latency.

However, as indicated by the small difference in mean saccadic endpoint between penalty 0 and penalty 500 trials, the visual properties of the stimulus configuration which interfere with the optimal execution of the eye movement are never fully ignored, even in trials with long saccadic latencies.

C. Processing of Reward and Optimality

There is an important difference between our study and the electrophysiological approaches described above [9,12,13,18]. These studies used the saccadic eye movement as an indicator for a decision process in the presence of color-coded reward information that could have also been accomplished, for instance, by a button press in a comparable manner. Here we explored the limits of the fine tuning of the saccadic system by directly linking the exact endpoint of the saccade to a reward or a loss. Thus, planning and executing an eye movement in our task led to consequences on a very fine spatial scale rather than making a choice by performing a saccade to the right versus to the left (see also [24] for an example of a pointing choice task).

Our study is not the only study in which computational models have been applied to understanding the processes and limits of processing of visual and reward information during motor control tasks. Recent work by Geisler and colleagues combines Bayesian modeling with human psychophysics to study human visual search strategies [4,52,53]. The optimal search strategy of this Bayesian Ideal searcher is defined as the strategy that maximizes the visual information collected across successive eye movements. In particular, the search strategy of the Bayesian Ideal searcher is different from the search strategy of a feature-based maximum *a posteriori* (MAP) searcher that plans the next eye movement toward the position in the display that contains the target with highest probability [54]. While the MAP searcher plans his/her next eye movement to the most likely target location, independent of information collected during previous fixations, the Bayesian Ideal searcher will search the display in order to maximize information about the available visual information.

An experimental comparison between human visual search behavior and the predictions for the Bayesian Ideal searcher for a target embedded in a noisy display showed that human searchers employ highly efficient search strategies that are very similar to the search strategies of the proposed Bayesian Ideal searcher [4,52,53]. Human search strategies differed from the predictions for the Bayesian Ideal searcher in two ways: First, the model in general underestimated saccade amplitudes and the increase in the number of fixation for eye movements toward targets presented at larger eccentricities, and second, the model failed to account for the spatial inhomogeneities in the distribution of fixations across the search display [52,53]. Some of the differences between the predictions by the Bayesian Ideal searcher model and the observed fixation pattern are likely due to the asymmetric enhancement of apparent contrast with shifts in spatial attention [33,55]. Consistent with the model predictions for a Bayesian Ideal searcher, expectations about scene context bias observers' fixation strategies toward more fixations into regions with expected context [54,56,57].

In order to plan an eye movement to the visual target in our task, subjects had to process not only visual information but also the color-coded reward information that clearly distinguished target from penalty information. Our results show that, with sufficient time for processing of stimulus and reward information, saccadic eye movements under risk can be planned with high efficiency, nearly maximizing expected gain. The fastest latencies executed in our study fell into the range of 100 ms to 140 ms, i.e., the range of latencies for express saccades [58]. Performance for saccades with these fastest latencies was significantly suboptimal, indicating that these fastest eye movements were initiated without fully processing the displayed stimulus and reward information. Depending on the saliency of the target region and the magnitude of the penalty value, performance improved considerably, reaching near-optimal strategies after an additional time delay of approximately 35 ms. Thus, at least 35 ms seem to be needed to identify and process reward and color coding and to accurately plan and execute eye movements in our task. We would like to emphasize, however, that this measure is subject to a considerable amount of variability and can range from being optimal even with very short latencies in some conditions to about 100 ms additional time for processing of reward-related information to achieve optimal performance maximizing expected gain in other conditions. We speculate that this difference in latency between the fastest, suboptimal express saccades and slightly slower nearoptimal saccades is needed to reliably recognize the target and to process the information about the assigned possible rewards and losses.

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