Eye movements during rapid pointing under risk

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Abstract

We recorded saccadic eye movements during visually-guided rapid pointing movements under risk. We intended to determine whether saccadic end points are necessarily tied to the goals of rapid pointing movements or whether, when the visual features of a display and the goals of a pointing movement are different, saccades are driven by low-level features of the visual stimulus. Subjects pointed at a stimulus configuration consisting of a target region and a penalty region. Each target hit yielded a gain of points; each penalty hit incurred a loss of points. Late responses were penalized. The luminance of either target or penalty region was indicated by a disk which differed significantly from the background in luminance, while the other region was indicated by a thin circle. In subsequent experiments, we varied the visual salience of the stimulus configuration and found that manual responses followed near-optimal strategies maximizing expected gain, independent of the salience of the target region. We suggest that the final eye position is partially pre-programmed prior to hand movement initiation. While we found that manipulations of the visual salience of the display determined the end point of the initial saccade we also found that subsequent saccades are driven by the goal of the hand movement.

Introduction

Eye and hand movements have been found to be tightly coupled during rapid visually-guided pointing. Here we report evidence that suggests that eye movements are not necessarily anchored to the hand movement, but may initially deviate from the goal of the hand movement depending on the low level features of the visual stimulus configuration. We recorded eye movements in a rapid pointing task under risk in which the (optimal) final hand position differed from the visually most salient part of the display (Trommershäuser et al., 2003a,b).

Eye movements during rapid pointing movements have previously been studied in paradigms in which subjects pointed at targets among a small set of visually presented stimuli. In these experiments, arm movements are externally driven by the visual target position provided by the experimenter (see e.g., Desmurget et al., 1998, Sarlegna et al., 2003, Song & Nakayama, 2006). Typically, a saccadic eye movement is made to the visual target position shortly before the pointing movement is initiated (Prablanc et al., 1979). Under speeded response conditions, in which the subject is instructed to point as quickly as possible, eye movement onset typically precedes hand movement onset by 100 ms or less for targets with abrupt onset (see e.g. Binsted et al., 2001; Gribble et al., 2002). However, depending on the speed-accuracy requirements of the task or for continuously visible targets, hand movements sometimes start up to 100 ms in advance of eye movements (Carnahan & Marteniuk, 1991; Gribble et al., 2002; Abrams et al., 1990). Saccades to new targets flashed during a pointing movement are typically postponed until the hand reaches the first target location (Carey, 2000; Neggers & Bekkering, 2000, 2002).

However, eye movements recorded under natural conditions do not exhibit this tight coupling. Subjects dedicate visual resources to grasp a needed object only for as long as needed, and the eye departs early from the target, when the action can be completed using proprioceptive control alone (Hayhoe et al., 2003; Pelz et al., 2001). Compared to more controlled laboratory experiments, observed eye-hand latencies in these experiments are much more variable ranging over a time window of 500-600 ms, with the hand sometimes even preceding fixation by as much as 250 ms (Pelz at al., 2001). Observed fixation durations seem to be determined by momentary task demands such as accuracy or exploratory behavior to generate a representation of the workspace (Hayhoe et al., 2003; Johansson et al., 2001; Pelz et al., 2001, Sailer et al. 2005).

Here, we recorded eye movements during movement under risk. Subjects received feedback about the end position of their finger pointing movement. Hits into a visually specified target region led to positive feedback (100 points). A penalty region abutted or even overlapped the target region. Hits into the penalty region incurred a penalty (0, -100 or -500 points). *Late responses* that reached the screen later than 700 ms were penalized (-700 points). Subjects did not receive feedback about their eye movements. Under these conditions, subjects have been demonstrated to choose optimal visuo-motor strategies maximizing expected gain (Trommershäuser et al., 2003a).[1]

Due to the imposed short time constraint for the pointing response, movement execution in our task is corrupted by considerable motor noise (see also Harris & Wolpert, 1998). A subject has to take this motor variability into account in planning his or her motor response. This implies aiming away from the penalty region, if the penalty region carries losses. As illustrated in Fig. 1a, the optimal motor response is shifted towards the right of the target center for a penalty region displayed toward the left. This shift is larger for higher penalty values and if penalty and target region are closer.

In our first experiment, the penalty region was a red disk (a third of the luminance of the background), while the boundary of the target region was indicated by a thin green circle, such that the fill of the target region matched the background in luminance and color. In subsequent experiments, the saliency of the stimulus configuration was varied. We understand manipulations of the saliency of the stimulus configuration as variation of low level features of the visual stimulus, such as changing the color and luminance of penalty and target region, and by using a disk to indicate the target region and a circle to indicate the penalty region. We introduced these manipulations to see whether they effect the saccades, the pointing movements, or both.

We find that, independent of the final hand position, initial saccades are always directed into the visually most salient part of the display. A second saccade follows, shifting away from the visually salient part towards the non-visually defined optimal touch point of the finger maximizing gain. Initial and second saccades are spatially coupled with the hand movement. The distance between first saccadic end point and finger end point decreases for saccades initiated with slower latencies, suggesting that the final eye position is partially specified prior to the initiation of the first saccade.

Methods

Apparatus

Subjects were seated in a dimly lit room in front of a 21-inch touch screen computer monitor *(ELO TouchSystems ET2125C,* resolution 1280 x 960 pixels @ 100 Hz). A chin rest was used to control the viewing distance, which was 48 cm from the subjects' eyes to the front of the touch screen. A *Microsoft* game pad was mounted on the table centered in front of the monitor at a distance of 39 cm and provided the start position of the movement. The experiment was programmed in C and run on a Pentium IV Dell Precision workstation. A calibration procedure was performed before each session to ensure that the touch screen measurements were geometrically aligned with the visual stimuli.

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).

Stimuli

Stimuli consisted of a penalty circle and a target circle and were presented on a grey background (luminance: 48 cd/m^2). The target and penalty circles had radii of 28 pixels / 9 mm / 1 deg. Both circles were color coded and overlapped by 0, 4.5 or 9 mm. The penalty circle appeared at one of six possible horizontal offsets with respect to the target (near, middle or far spatial condition, see Fig. 1b). The penalty for hitting inside the penalty region was fixed within each block of 24 trials and alternated between 0, 100 and 500 points across the 18 blocks.

The visual salience of the stimulus configuration was varied by changing the color of the visual stimulus configuration. The color of target and penalty regions changed from initially green (target) and red (penalty) to either black or blue. With the exception of one condition ("background luminance"), either target or penalty region were a filled (disk) or hollow circle. In the condition “background luminance”, target and penalty regions were indicated by thin hollow circles, such that the inside of the circle matched the background color and luminance. Stimuli were presented at a minimum distance of 3 deg in horizontal and vertical direction and a maximum distance of 7.5 deg in horizontal and vertical direction from initial fixation in the center of the screen to facilitate saccadic responses towards the stimulus. The spatial position of stimulus presentation on the screen was chosen randomly on each trial to prevent subjects from relying on preplanned movement strategies.

Procedure

Each trial followed the procedure illustrated in Fig. 2. The display of a fixation cross in the screen center indicated the start of the trial. The subject was required to depress the button on the game pad with the same finger that she/he would later use for the pointing movement. While the subject held the button pressed, the fixation cross changed its color from black to white indicating that the stimulus configuration would be displayed shortly. This period until stimulus display varied randomly between 400 and 600 ms. The display of the target configuration marked the beginning of the time window available for the hand movement response. Subjects were required to release the start button and touch the screen within 700 ms or they would incur a loss of 700 points. With the exception of one condition (“open loop”, see below), the stimulus configuration was displayed until the subject touched the screen. If the subject touched the screen 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 subject’s total accumulated points for that session. A hit on the target circle gained 100 points. The penalty for touching the penalty circle was constant during a block of trials, and could amount to a loss of 0, 100 or 500 points. If the screen was touched in the region of overlap between the target and penalty circles, the reward and penalty were combined.

Each block of trials consisted of 4 repetitions of each of the six stimulus configurations, presented in random order. A single experimental session consisted of a touch screen calibration, 12 warm-up trials, and eighteen blocks of 24 trials. The penalty level was fixed in each block, and alternated in ascending order (0, 100, 500, 0, 100, 500 and so forth) across the 18 blocks. Subjects repeated the calibration of the eye tracking system every 72 trials to ensure high calibration accuracy during the experiment (averaged spatial saccadic error ~ 0.2 degrees).

The experiment was also run under three control conditions, two of which were conducted to separate visual and pointing response. In the first control condition ("open loop"), the stimulus configuration was removed at the time of initiation of the hand movement. In the second control condition ("visual judgment"), subjects performed a visual judgment task, indicating whether the target was on the right side or the left side of the penalty by performing a pointing movement into the corresponding right or left half of the screen. In the third control condition ("fixation"), subjects were instructed to maintain fixation at screen center during the pointing response.

All subjects performed an initial training session of 270 trials to learn the speeded response task. During the training session the overall time limit for the response decreased across 270 trials. In the first 30 trials of the training session, there was no time limit for completing the pointing movement and no penalty for hitting the penalty region. This was followed by 4 blocks of 24 trials each with a time limit of 850 ms and penalty values of 0 and 100 points, alternating between successive blocks.

In the final 6 blocks, the time limit was 700 ms; the penalty values again alternated between blocks.

Eye movements were recorded during all phases of the experiment, except for the training session and the 12 warm-up trials of each session. In each trial, the recording of eye movements started with trial initiation, i.e. the display of the fixation cross at screen center and stopped when the subject touched the screen. Subjects were instructed to maintain fixation at screen center at the beginning of each trial or the trial would not start. Subjects received no instructions about where to direct their eyes, except in the “fixation” condition in which subjects maintained gaze at screen center.

Subjects

12 subjects participated in this study. The subjects were 4 male and 8 female members of the Department of Psychology of the University of Giessen or students at the University of Giessen. All participants but one were right-handed, all had normal or corrected-to-normal vision and ranged from 20 to 35 years in age. Subjects used their dominant hand for the pointing response. All but one subject (MS, the first author) were unaware of the hypotheses under test. Each experimental session lasted 444 trials (12 warm-up trials, 18 blocks of 24 trials). Subjects needed approximately 45 minutes to complete each session. Subjects were informed of the payoffs and penalties for each block of trials. Subjects were also informed about their current cumulative score after each trial and competed for the overall high score. All subjects had given their informed consent prior to testing and were paid 8 € per hour for their participation in the experiment. The points won by the subjects were not converted

into a monetary bonus, however, a competitive environment was created by posting the high score list of total accumulated winnings in the lab.

Data Analysis

For each trial, we recorded finger reaction time (time from stimulus onset until the subject released the button), finger movement time (time from button release until the subject touched the screen), finger end point position on the screen, the score, saccadic reaction times, fixation duration and eye position. Analyses of the saccades focused on the end points of the first and second saccades. In a limited number of trials (less than 10%), subjects made more than two saccades. These trials were not excluded, but in all trials, only first and second saccades were analyzed. Third saccades were always very small and did not provide additional information for the purposes of the study. Trials in which the subject released the button of the game pad earlier than 100 ms after display of the stimulus, or hit the screen later than 700 ms after stimulus display were excluded from the analysis. Each subject contributed at least 360 data points, i.e. 20 repetitions per condition. Subjects' performance was compared to a model of optimal movement planning based on each subject's measured finger end point variability (see below).

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) and analyzed offline using *Matlab* routines. The standard *Eyelink II* criterion was used for saccade detection. The *Eyelink II* saccade parser computes instantaneous eye velocity and acceleration and compares these to velocity and acceleration thresholds (22 deg/s and 2000 deg/s^2).

Model of Optimal Movement Planning

Subjects' pointing responses were compared to a model of optimal movement planning based on statistical decision theory (Trommershäuser et al., 2003a,b). In this model, an optimal visuo-motor movement strategy is defined as the motor strategy maximizing expected gain.

The model takes into account explicit gains associated with the possible outcomes of the movement, the mover's own task-relevant variability, the possibility of visual feedback and the costs associated with the time limits imposed on the mover. For the conditions of our experiment, the expected gain of motor strategy S is defined by

$$\Gamma(S) = \sum_{i=1}^{2} G_i\, P(R_i|S) + G_{\text{timeout}} P(\text{timeout}|S), \qquad (1)$$

where $P(R_i \mid S)$ is the probability, given a particular choice of strategy S, of hitting the target region R_1 or the penalty region R_2 before the time limit has expired (t = timeout). The last term captures the penalty and probability of a timeout. In our experiment subjects rarely timed out in completing their movements once they were practiced with the time constraints of the task. As a result, the last term in Eq. 1 is close to zero and can be dropped in determining the maximum expected gain (MEG) strategy.

In this model, the visuo-motor strategy S is identified with the mean finger end point on the screen $(\bar{x},\bar{y})$. We find that movement end points are distributed around this mean according to a bivariate Gaussian distribution,

$$p(x,y \mid \bar{x},\bar{y},\sigma_x,\sigma_y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left[-\left(x-\bar{x}\right)^2 \big/ 2\sigma_x{}^2\right]\cdot\exp\left[-\left(y-\bar{y}\right)^2 \big/ 2\sigma_y{}^2\right]. \qquad (2)$$

Once subjects are practiced in the task, the variance is isotropic $\sigma^2 = \sigma_x^2 = \sigma_y^2$ and remains constant throughout the experiment (i.e., independent of the mean end point, spatial and penalty conditions; Trommershäuser et al. 2003a). The probability of hitting region R_i is then defined by the choice of $(\bar{x},\bar{y})$ on the screen and the subject's end point variability σ as

$$P(R_i|\bar{x},\bar{y}) = \int_{R_i} p(x,y\,|\,\bar{x},\bar{y},\sigma)\,dx\,dy\ . \tag{3}$$

Under these assumptions, the optimal movement strategy corresponds to the mean end point $(\bar{x}_{\mathrm{MEG}},\bar{y}_{\mathrm{MEG}})$ maximizing

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

In our experiment, this MEG strategy $(\bar{x}_{MEG},\bar{y}_{MEG})$ varies with the position and magnitude of the penalty. When the penalty is zero, the optimal mean end point position is the center of the target region (Fig. 1a). For non-zero penalties, the optimal mean end point 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 subjects with greater motor variability σ (see also Trommershäuser et al. 2003a,b).

Comparison of human and optimal performance

Human performance was compared to optimal performance for each subject individually based on the measured end point variability and Eq. (1). The model predicts large shifts in mean movement end points when the penalty is large and not far from the target (Fig. 1a). So, when discussing the results we mostly focused on penalties of 500 and on the near configurations.

We compared subjects' performance to optimal performance by computing the overall efficiency in our task. Efficiency in our task is defined as the total actual score divided by the optimal score derived from the model of optimal movement planning.

Performance was classified as significantly different from optimal when the actual score fell outside the 95% confidence interval of optimal performance. The range of optimal scores was computed in a Monte Carlo simulation consisting of 100,000 runs of the optimal movement planner performing the experiment with each subject's variance (for the equivalent number of conditions and repetitions).

Results

Initial saccadic eye movements are not anchored to the hand movement during rapid movement under risk

As long as target and penalty region were visible throughout the movement, subjects completed two saccades on average before the finger hit the screen. First saccades were initiated with median latencies of approx. 130 ms, followed by a second saccade after an average fixation duration of 140 ms (Fig. 3). Second saccades were completed approximately 300 ms before the finger hit the screen (Fig. 3b). We find that, independent of the final hand position, initial eye movements were executed into the visually most salient part of the stimulus configuration. This initial eye movement was followed by a second saccade, shifting away from the visually salient part towards the non-visually defined touch point of the finger that would maximize expected gain (Fig. 4).

The average number of saccades per trial ranged from 1.94 ± 0.63 (penalty red disk condition) to 2.32 ± 0.99 (background luminance condition), and dropped significantly below 2 (1.58 ± 0.72) under open loop conditions when the stimulus was removed at movement onset (Results of ANOVA, $F(3, 5298) = 102.9$; $p < 0.001$; average number of saccades in the open loop condition was significantly different at the 0.05 level; Scheffe-Test, data pooled across subjects). The average number of saccades per trial was lower for trials in which the first saccade landed closer to the finger touch point (Fig. 5). (The mean number of saccades of the lower quartile of the distribution of distances from first saccadic end point to the finger touch point in this condition was significantly different from the mean number of saccades of the upper quartile of the distribution; t-Test, $t=15.17$, $p<0.001$, $df=812$). This was the case for all spatial, penalty and saliency conditions tested.

In most trials, a second successive saccade was executed in the direction of the touch point of the finger with a mean angle of 5° between the direction of the second saccade and the vector between the end point of first saccade and the finger touch point (Fig. 6 and 9a). The mean angle between the direction of the second saccade and the vector connecting end point of first saccade and optimal finger touch point was 4° (data not shown, distribution not significantly different from the distribution of angles in Fig. 6, t-Test, $t=0.869$, $p=0.385$, $df=1278$).

Under open loop conditions, finger end point variability increased from $\sigma = 2.6$ mm under free viewing conditions (individual subject variabilities: $\sigma = 1.8$ to 3.2 mm, 4 subjects) to $\sigma = 4$ mm (individual subject variabilities: $\sigma = 3.4$ mm to 4.4 mm, 4 subjects).

In all conditions of the experiment, the vast majority of initial saccadic responses landed in the region of the disk. This was the case, irrespective of whether this region was the penalty or the target region, whether subjects responded by pointing at the stimulus configuration or simply judged the relative position of the penalty circle. (Fig. 7; number of initial saccades / mm^2 in the region of higher visual saliency is significantly higher than the number of saccades / mm^2 anywhere else on the screen; t-Test, t=11.5, p = 0.001, df=3, data pooled across the four left conditions displayed in Fig. 7). In the condition in which target and penalty region were indicated by hollow circles and the fill of the circles was of the same color and luminance as the background, saccadic density was still higher in the penalty and target region, compared to the background, indicating that subjects had no difficulty localizing the stimulus configuration in this condition (Fig. 7).

The latency of the first saccade (i.e. the time from stimulus onset until the eye starts moving) did not depend on penalty value (Results of ANOVA, F(2, 1626) = 0.18; p = 0.982). However, reaction time of the hand did depend on the loss associated with hitting inside the penalty region (Results of ANOVA, F(2, 1626) = 4.693; p = 0.009; hand reaction time in the penalty 0 condition was significantly different from hand reaction time in the penalty 100 condition (250 ms versus 257 ms) at the 0.05 level; Scheffe-Test, data pooled across subjects). The mean hand reaction time in the penalty 500 condition was 254 ms and was not significantly different from either of the other penalty conditions. Movement times of the hand were slightly faster in the penalty 500 condition (352 ms) than in the penalty 100 condition (354 ms) or penalty 0 condition (358 ms). This difference was significant for the penalty 500 condition (with respect to the penalty 0 condition; Results of ANOVA, F(2, 1626) = 4.686; p = 0.009, data pooled across subjects).

Initial saccades ended closer to the finger end point when initiated with slower latencies (Fig. 8a). The average distance between first saccade and touch point of the finger ranged from 11.3 mm (SEM 0.16 mm) in the background luminance condition to 12.4 mm (SEM 0.18 mm) in the penalty black disk condition. This distance was smaller for saccades that were initiated with slower latencies and larger for saccades with faster latencies (Fig. 8a; mean distance from the end point of the first saccade to the touch point of the finger of the lower quartile of the distribution of latencies first saccades significantly different from the distance from the end point of the first saccade to the touch point of the finger of the upper quartile; t-Test, $t=27.8$, $p<0.001$, $df=89$). This was the case for all spatial, penalty and saliency conditions tested. Accordingly, latencies of the first saccade correlated significantly with the distance from the end point of the first saccade to the touch point of the finger ($r = -0.282$, $p < 0.01$, see Fig. 8b).

Latencies of the first saccades correlated moderately with latencies of the hand (correlation between eye and hand latencies ranging from 0.10 to 0.25; correlations, pooled across all 4 subjects, computed separately for each penalty and spatial condition; r-values statistically significant ($p < 0.05$) in all but two of 9 cases). Saccadic end points of the first saccade correlated significantly with the finger touch point (correlation between saccadic and finger end point in x-direction ranging from 0.15 to 0.28; correlation between saccadic and finger end point in y-direction, ranging from 0.32 to 0.54; correlations computed across 4 subjects separately for each condition; $p < 0.05$ in all but two of 18 cases). Saccadic end points of the second saccade exhibited slightly lower, but still significant trial-by-trial correlations with the finger end points (correlation between saccadic and finger end point in x-direction: ranging from 0.01 to 0.25; correlation between saccadic and finger end point in y-direction, ranging from 0.18 to 0.33 for the different spatial and penalty conditions; correlations computed across 4 subjects separately for each condition; $p < 0.05$ in all but two of 18 cases).

Subjects' performance drops below optimal under open loop pointing and constraint of fixation

Subjects always chose near-optimal visuo-motor strategies maximizing expected gain by shifting the mean finger movement end point away from the penalty in response to penalty values > 0 (Fig. 9a and 9b), independent of the color of the stimulus and independent of whether they pointed at a target disk or circle (comparison of movement end points across the two saliency conditions, penalty red disk, and target green disk, $p = 0.501$ (Penalty 500), $p = 0.309$ (Penalty 100), $p = 0.066$ (Penalty 0); data pooled across 4 subjects and all spatial conditions; Bonferroni-corrected for 3 tests). Subjects' performance varied between 78 and 92 points per trial under unconstrained viewing conditions, and dropped significantly in the open loop condition (performance ranging between 36 and 75 points per trial) and in the fixation condition (performance ranging between 48 and 80 points per trial). Subject efficiencies varied between 91% (TS) and 98% (VC) percent, which is slightly lower than found in previous studies (Trommershäuser et al., 2003a,b; Trommershäuser et al., 2005). Efficiency was significantly sub-optimal under open loop conditions in which the configuration was not visible during the movement (54% for VC to 86% for MSP, see also Fig. 9c) and when subjects were asked to maintain fixation at screen center (85% for CF to 91% for BW). These results replicate previous studies, in which subjects have been found to choose visuo-motor strategies nearly maximizing gain under unconstrained viewing conditions (Trommershäuser et al., 2003a,b).

Subjects' performance turned into grossly sub-optimal performance under open loop conditions and when subjects were instructed to maintain fixation at screen center throughout the pointing movement. Subjects failed to shift their movement end point from the target center when the stimulus was removed upon movement initiation

(Fig. 9b). Pointing variability also increased under fixation at screen center from $\sigma = 2.6$ mm under free viewing conditions (individual variability ranging from 1.8 mm to 3.2 mm) to $\sigma = 5$ mm (individual variability ranging from 3 mm to 6 mm). This effect is most likely caused by an increased amount of sensory noise for stimulus presentation in the periphery (Bekkering & Sailer, 2002; Henriques & Crawford, 2000). In summary, optimal performance was disrupted by removal of stimulus information with movement onset or by sustained stimulus presentation in the periphery due to the constraint of fixation to the screen center.

Discussion

Eye movements are driven by visual features of the stimulus and the hand movement

We recorded eye movements during rapid pointing movements under risk. Subjects pointed at stimulus configurations that consisted of two visual stimuli, a green target region and a red penalty region. Hits into the target region earned a monetary reward, hits into the penalty region incurred a loss. While the penalty region was a color-coded disk, the target was indicated a by a circle. Subjects chose near-optimal visuo-motor strategies maximizing gain by pointing towards the outer edge of the transparent target circle in opposite direction from the penalty disk. The recorded pattern of eye movements indicated that subjects directed their gaze initially towards the region of high visual saliency, followed by a saccade into the direction of the touch point of the finger. Thus, when changing the penalty region to a circle and the target region to a disk, initial eye movements shifted to the filled region.

Our results contradict findings from previous studies in which eye movements were found to be anchored to the hand movement goal until the pointing movement was completed (Carey, 2000; Neggers & Bekkering, 2000, 2002), The reason for this difference between the results found in our study and the results by Neggers & Bekkering (2000, 2002) can be explained by the fact that in our experiments the hand movement goal was not defined “purely visually” by a shifted visual target. Instead, here, subjects pointed at, or close to, a hand movement goal maximizing gain. This optimal point of maximum gain is defined by the subjects’ own motor variability and by the points assigned to target and penalty region, and differs spatially from the luminance defined center-of-gravity of the stimulus configuration, i.e. from the center of the filled disk. The eye movements recorded under these conditions are not tightly anchored to the hand movement as found by Neggers & Bekkering (2000, 2002), but deviate into the visually most salient part of the display. Our results rather match the results observed in the context of visual search paradigms, in which initial eye movements have been found to be directed at the center-of-gravity of the stimulus configuration (e.g., Najemnik & Geisler, 2005; Zelinsky, 2001; Schall, 2003).

In the context of our study, we are referring to low level manipulations of the stimulus, such as color or contrast as variations of visual salience. However, the term “visual salience” is not unambiguously defined in the literature. In general, visual saliency can be understood to be a composite of the low-level visual characteristics of a scene, with a high-saliency object being one of different color, contrast, luminance or orientation compared to its surroundings. Itti and Koch (2000, 2001) have argued that saliency is independent of the character of the experimental task, operates very rapidly and is primarily driven in a bottom-up fashion, although it can be influenced by contextual factors. If a stimulus is sufficiently salient it will clearly pop out of a visual scene and can be distinguished fairly easily from its background or surroundings. What seems to be important for the computation of saliency is feature contrast with respect to the contextual surround rather than absolute feature strength or other detailed characteristics of the features.

The visually salient stimuli in our study are defined by their difference in luminance or color compared to each other or to the background. Surprisingly, saccadic latencies of initial saccades in our task were very short and even shorter than saccadic latencies typically found in so-called gap trials in purely perceptual tasks in which the fixation stimulus is removed prior to stimulus onset (Dickov & Morrison, 2006; Fischer & Weber, 1998). In our task, subjects fixated for approximately 140 ms after this initial saccade before initiating the hand movement and shifting their second saccade into the direction of the finger touch point. This fixation interval between first and second saccade is about 60 to 80 ms longer than the time of suppression of visual information prior to eye movement initiation (Duffy & Lombroso, 1968; Caspi et al., 2004).

Information about the optimal hand position maximizing gain builds up within 300 ms following stimulus presentation

It has been suggested that the parietal cortex might be involved in the allocation of spatial attention and motor intention (see, e.g., Andersen & Buneo, 2002; Colby & Goldberg, 1999; Bisley & Goldberg, 2003). In accordance with these results, there is evidence from a number of studies on human subjects that the posterior parietal cortex topographically codes spatial attention to action-relevant locations and is involved in the spatial programming of saccades (Curtis & D'Esposito, 2006; Schluppeck et al., 2005; Sereno, et al., 2001; Silva et al., 2005; Yantis et al., 2002).

In our task, initial saccades are followed by a second saccade towards the optimal touch point of the hand, i.e. completed approximately 300 ms prior to arrival of the hand at the screen. This second saccade is typically initiated 30 - 40 ms after initiation of the hand movement and approximately 300 ms after visual information about the goal configuration is first available. We suggest that the hand latencies of around 260 ms indicate the minimum time to compute the goal of the hand movement, i.e. generate a representation of maximum expected gain. This time is slightly shorter than the time constant of modulation of neural activity seen in monkey single cell recordings from the intra-parietal cortex during saccadic choices (Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Sugrue et al., 2004), but significantly longer than the time until initiation of the first initial saccade. Findings from visual search tasks suggest that visual information can be accumulated simultaneously for the first and second saccade prior to initiation of the first saccade (Caspi et al., 2004). Hence initial saccades directed at the luminance defined center-of-gravity in our task may be executed to add much needed spatial information about the relative position of target and penalty region.

Finally, eye and hand latencies observed in our task were more than 100 ms shorter than observed during rapid pointing movements directed at simple stimuli (Morrone et al., 2005; Neggers & Bekkering, 2000, 2002; Salegna et al., 2003). Eye and hand latencies have been demonstrated to decrease in the presence of reward (Galvan et al., 2005; Hikosaka et al., 2006). The short latencies found in our task may therefore reflect a motivational component due to the imposed time limit of only 700 ms for the pointing movement and due to repeated positive reinforcement during our experiment.[2]

We conclude that eye and hand movements are coupled to the goal of the hand movement during rapid movement under risk. However, eye movements are initially driven by low level visual features of the stimulus configuration and may serve target localization.

Figure captions

Fig. 1: Experimental Design. a) Optimal pointing strategy. The optimal aim point shifts away from the target center in the penalty 100 condition and in the penalty 500 condition compared to the penalty 0 condition. Results of simulations for a subject with aim point variability of 3.5 mm. **b)** Stimulus configurations. The target region was presented either to the right or to the left of the penalty region at three different offsets between target center and penalty center.

Fig. 2: Typical series of events in a trial. A trial started with a display of a fixation cross in the middle of the screen. Subjects pressed a button to initiate the trial, and the fixation point dimmed to indicate the stimulus configuration would soon be displayed. After a random time interval, the stimulus configuration was presented at a minimum distance of 3 deg from initial fixation (and a maximum distance of 7.5 deg). Subjects had a time window of 700 ms following stimulus presentation to complete their pointing response in order to avoid a penalty of -700 points / 7 cents.

Fig. 3: Typical timing of eye and hand. a) Average saccadic and hand latencies (pooled across 4 subjects). Typically, both saccades were concluded prior to completion of the hand movement. **b)** Distribution of saccadic and finger reaction times. Data pooled across 4 subjects and all 6 spatial and 3 penalty conditions.

Fig. 4: Saccadic end points and finger touch points. a) Typical eye trace during rapid pointing movement under risk. Eye trace (solid line), saccadic end points

(circles) and finger touch point (star) of subject MSP in the near configuration and penalty 500 condition (penalty: red disk, target: green circle). **b)** Spatial distribution of saccadic end points and finger touch points in the near configuration and penalty 500 condition (red penalty disk, target circle) for 4 subjects. Black circles indicate end points of the first saccades, red circles indicate end points of the second saccades, blue circles indicate the finger touch points, means are represented by the bold symbols (mean of the first saccades represented by the white symbol, mean of the second saccades represented by the red symbol, mean of the finger touch points represented by the blue symbol).

Fig. 5: Change in saccadic error with movement initiation. Average number of saccades for two different saliency conditions (red penalty disk / target circle; penalty circle / green target disk) and for two control conditions (open loop, i.e. stimulus display ends with finger movement onset, red penalty disk, target circle; background luminance: both circles are defined by a circle). Means computed across the first quartile and the forth quartile of initial eye-hand distance. Dashed lines indicate the average number of saccades per trial in this condition. Data pooled across 4 subjects and all 6 spatial and 3 penalty conditions. Error bars indicate ± one standard error of the mean.

Fig. 6: Direction of second saccade with respect to finger end point. The mean of the distribution is 5°. Data from the penalty red disk condition, pooled across 4 subjects and all 6 spatial and 3 penalty conditions.

Fig. 7: Density of saccadic end points. Saccadic density (first saccades) in regions with higher saliency (i.e. inside filled disk) and lower saliency (i.e. anywhere else on the screen) for the same conditions as in Fig. 5 and the visual judgment condition (subjects do not point at the stimulus configuration, but judge the relative position of the target circle). The light gray column on the right indicates saccadic density in the penalty region in the "background luminance" condition. Please note the logarithmic scale on the y-axis of the plot. Data pooled across 4 subjects and all 6 spatial and 3 penalty conditions.

Fig. 8: Distance between first saccade and finger end point. a) Decrease in distance between first saccade and finger end point with slower saccadic latency for the same conditions as in Fig. 5 and one saliency condition (penalty black disk, target circle). Means computed across the first quartile and the forth quartile of saccade latencies. Data pooled across 4 subjects and all 6 spatial and penalty conditions. Error bars indicate ± one standard error of the mean (computed across trials and 4 subjects). **b)** Correlation of latencies of the first saccade and the touch point of the finger. The black straight line indicates the linear regression, data shown for the target green disk condition, data pooled across 4 subjects.

Fig. 9: Actual pointing responses compared to the response of an optimal performer. a) Horizontal shift in finger end point away from the target center compared to the shift of an optimal performer for the red penalty disk condition. (squares: penalty 100, triangles: penalty 500). White symbols indicate no overlap between target center and penalty center, light grey indicates medium overlap, dark

grey indicates large overlap. Circles show the shift of the mean end point of the second saccade for each condition. Data pooled across 4 subjects. Error bars indicate ± one standard error of the mean. **b)** Horizontal shift in finger end point away from the target center compared to the shift of an optimal performer. Data displayed for the near configuration and penalty 500 condition for two conditions of visual saliency (diamonds: red penalty disk / target circle; squares: penalty circle / green target disk) and one control condition (triangles: open loop, i.e. stimulus display ends with finger movement onset, red penalty disk, target circle). Individual subjects are marked by identical symbols per condition. Subjects were compared individually to the model of optimal performance based on each subject's individual finger end point variability. **c)** The actual number of points won compared to the optimal score as predicted for an optimal performer in this experiment (scores pooled across all 6 spatial and 3 penalty conditions). Data displayed for two conditions of visual saliency (diamonds: red penalty disk / target circle; squares: penalty circle / green target circle) and one control condition (black triangles: open loop, i.e. stimulus display ends with finger movement onset, red penalty disk, target circle). Individual subjects are marked by identical symbols per condition. Subjects were compared individually to the model of optimal performance based on each subject's individual finger end point variability. Asterisks mark sub-optimal performance outside the 95% confidence interval of optimal performance.

Footnotes

1: Here, we denote monetary outcomes as gains (G_i), as commonly employed for gains/losses in statistical decision theory (Maloney, 2002, see also Glimcher, 2001) and we refer to outcomes as gains denoted with losses coded as negative gains. The term expected gain that we use corresponds exactly to expected value in the psychological literature.

2: All our subjects completed the experiment with an overall positive score.

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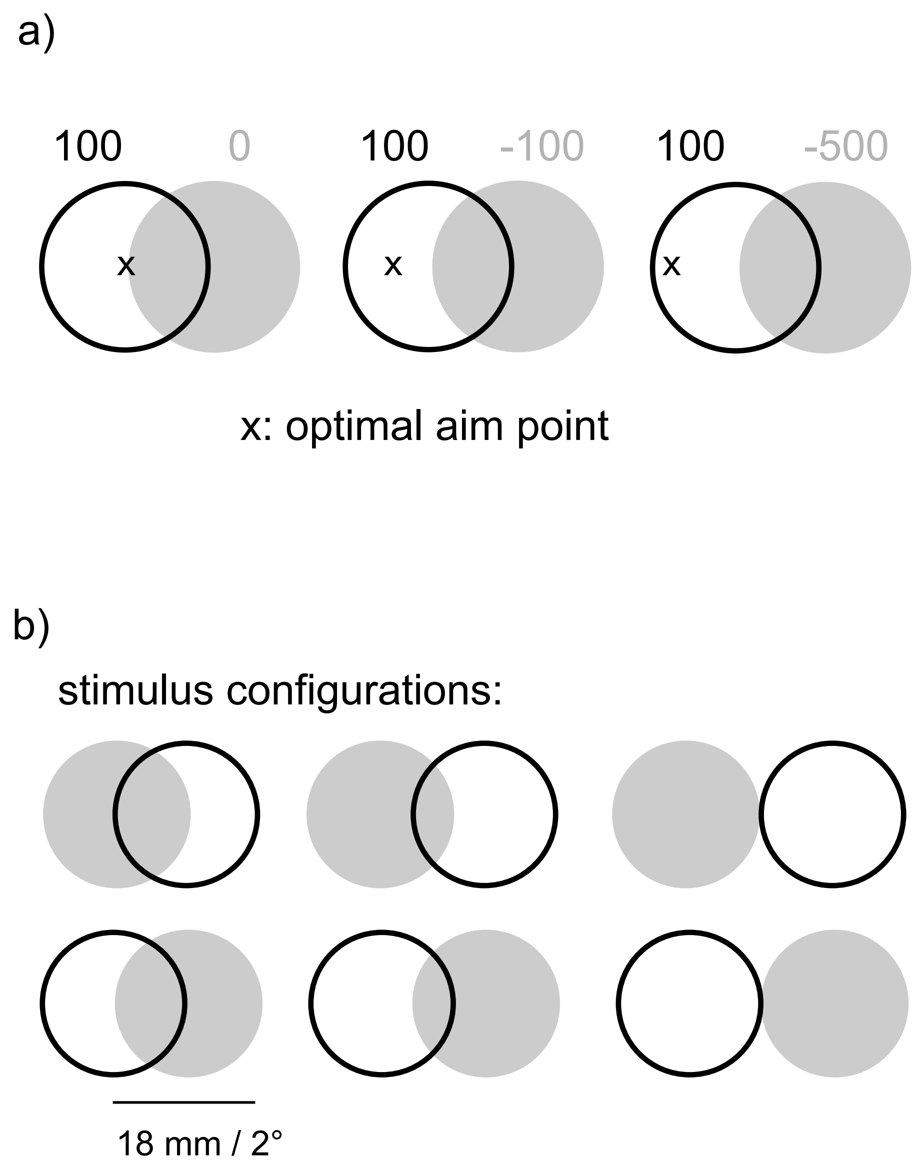

a)
100
0
100
-100
100
-500
x
x
x
x: optimal aim point
b)
stimulus configurations:
18 mm / 2°

Figure 1

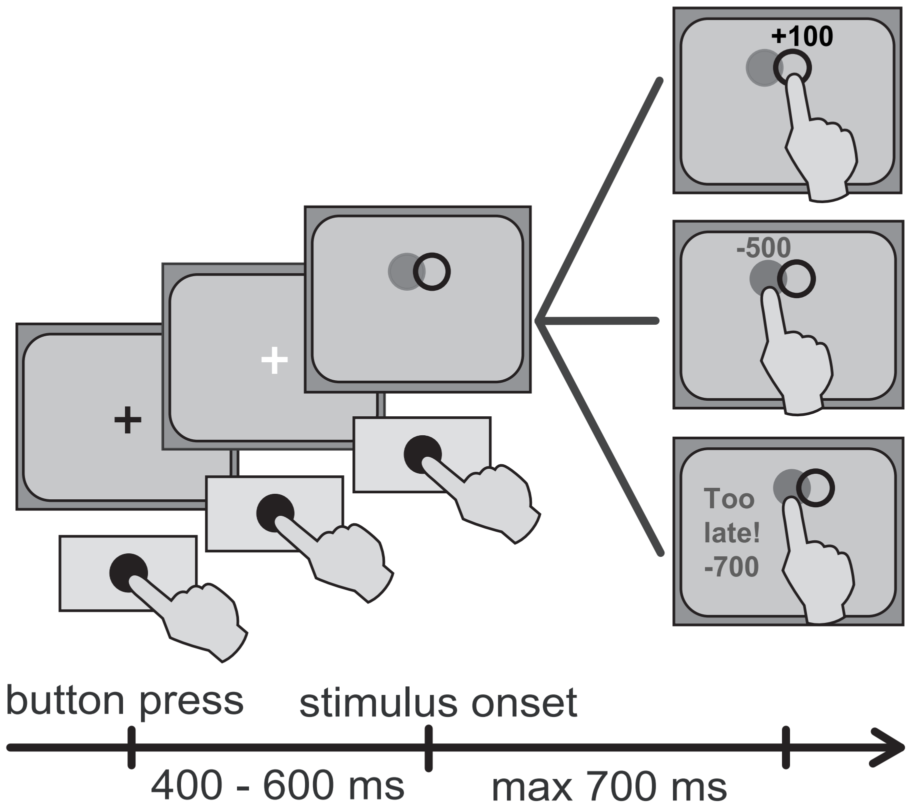
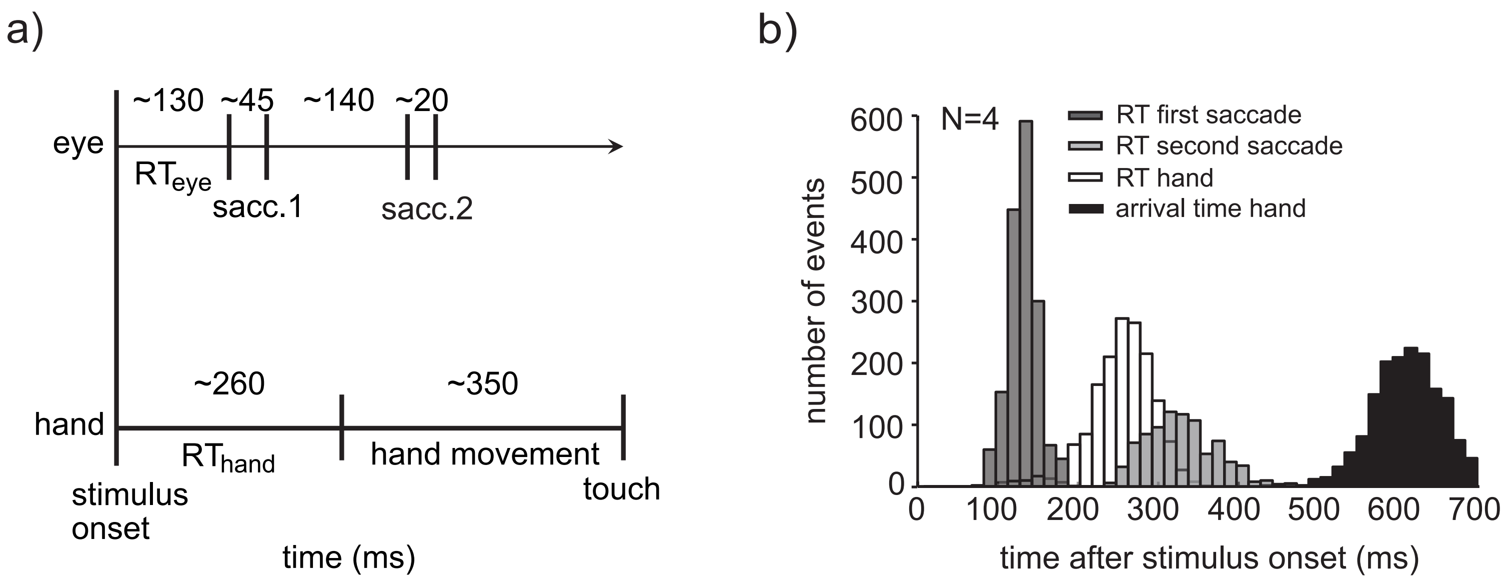

+100
-500
Too
late!
-700
button press
stimulus onset
400 - 600 ms
max 700 ms

Figure 2



a)
~130
~45
~140
~20
eye
RTeye
sacc.1
sacc.2
~260
~350
hand
RThand
hand movement
stimulus onset
touch
time (ms)
b)
N=4
RT first saccade
RT second saccade
RT hand
arrival time hand
number of events
600
500
400
300
200
100
0
0
100
200
300
400
500
600
700
time after stimulus onset (ms)

Figure 3

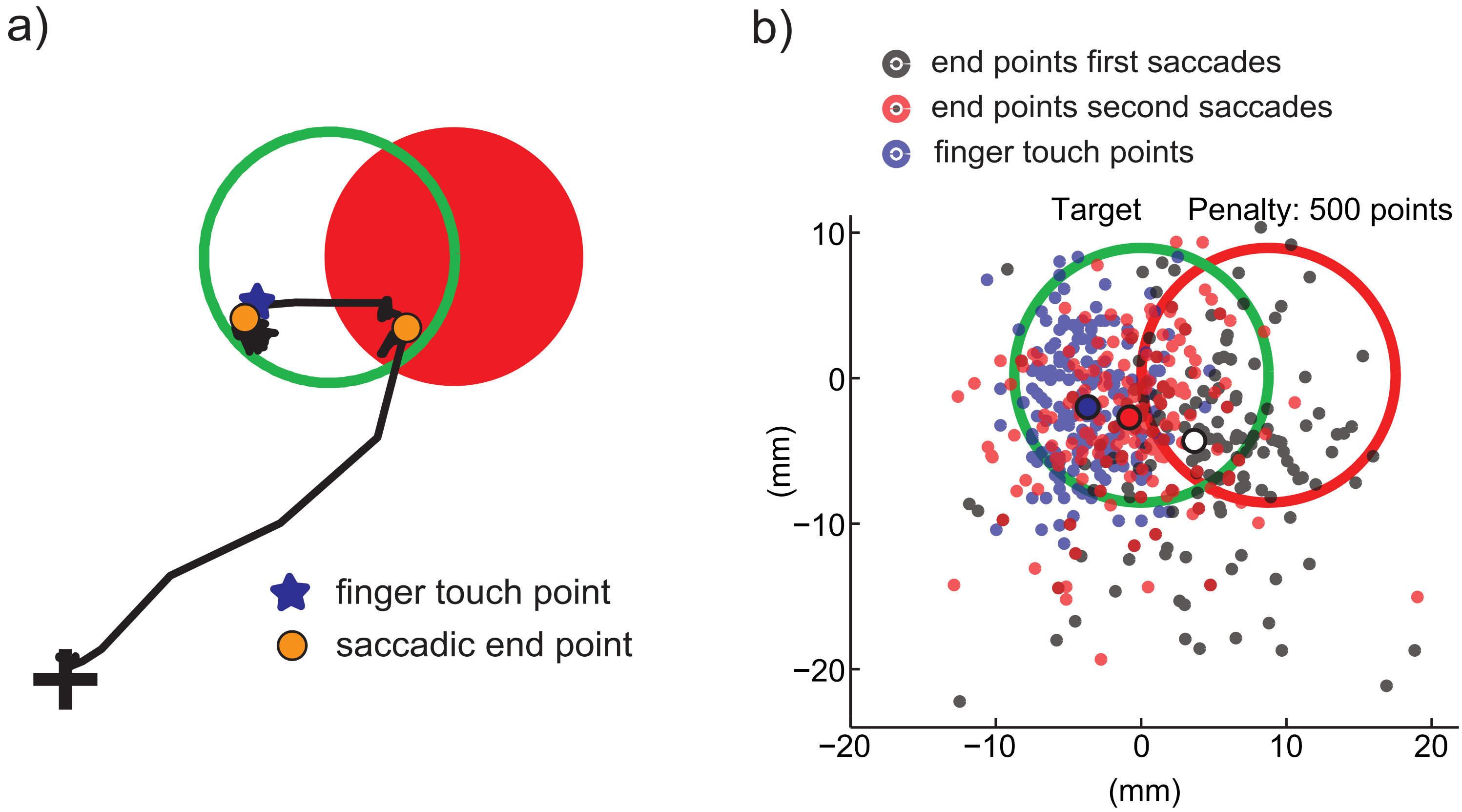
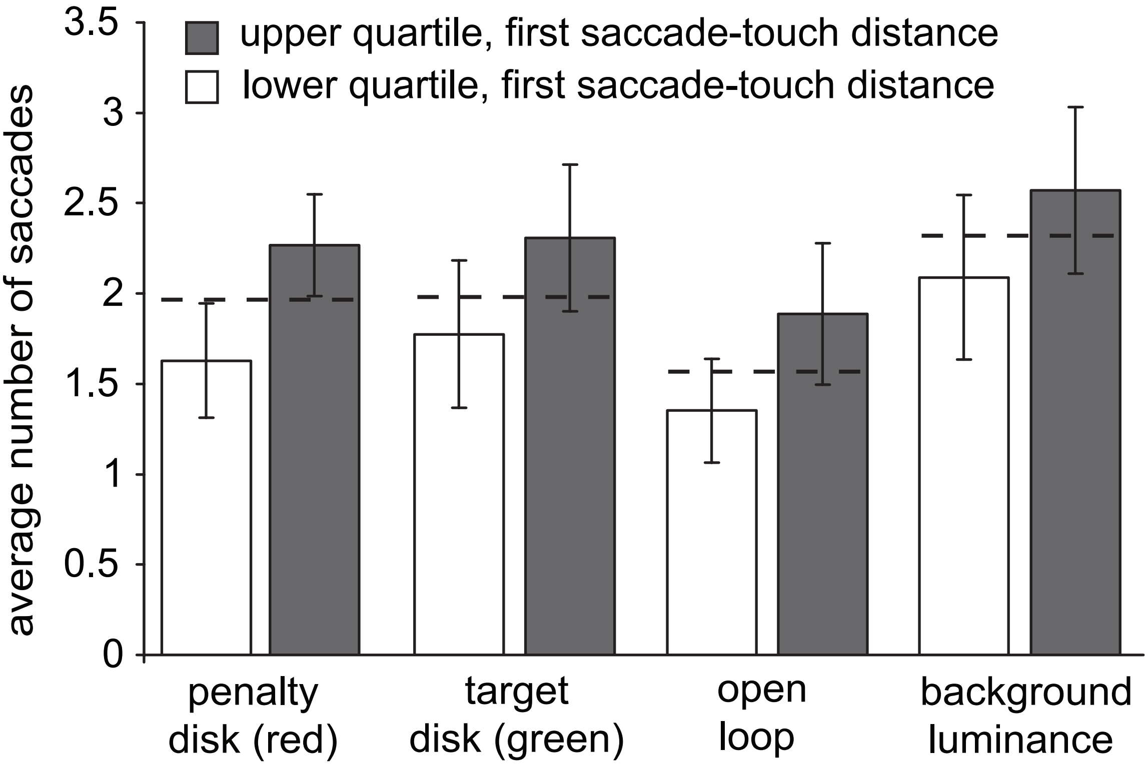
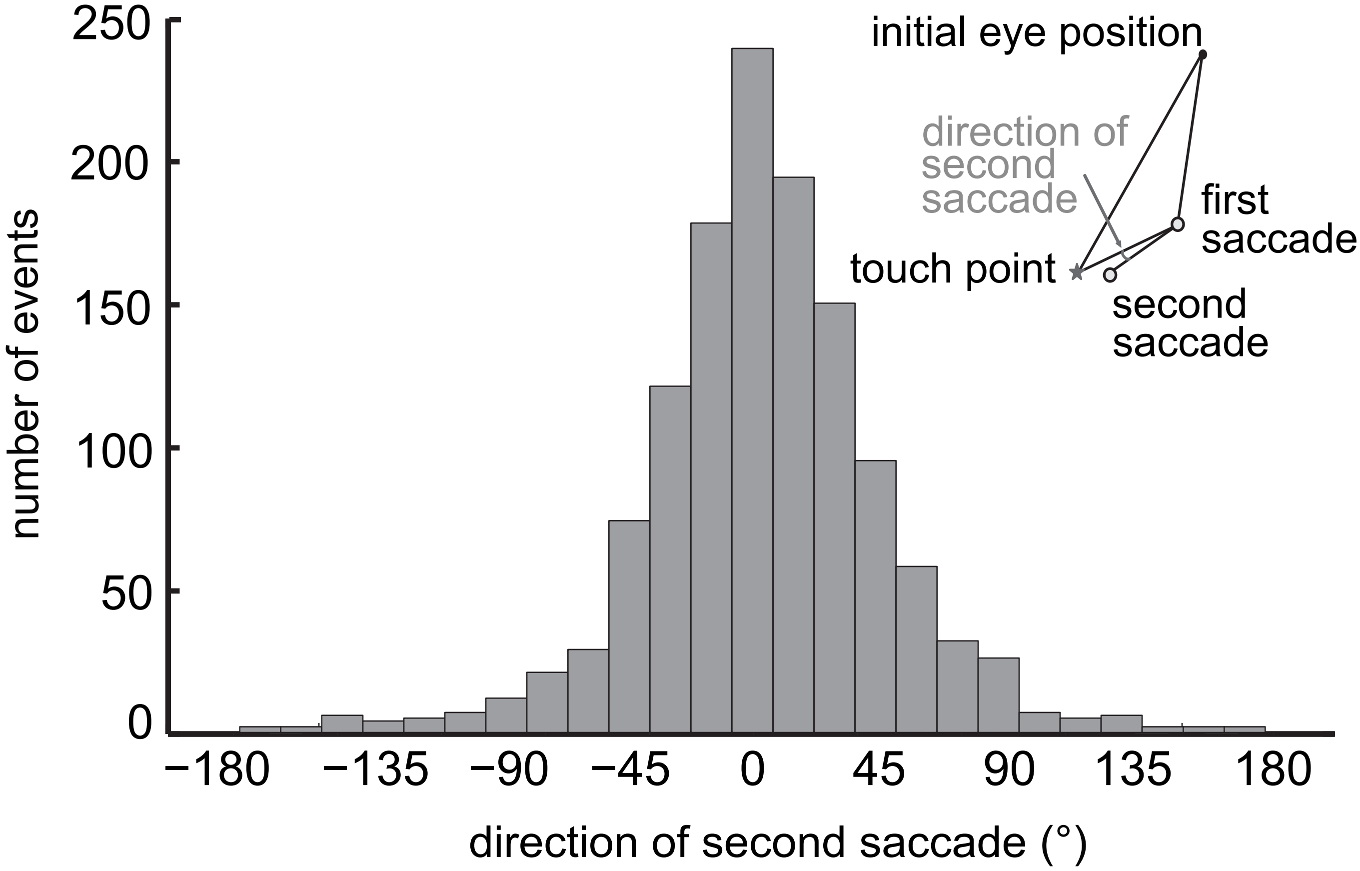

a)
finger touch point
saccadic end point
b)
end points first saccades
end points second saccades
finger touch points
Target
Penalty: 500 points
10
0
−10
−20
(mm)
−20
−10
0
10
20
(mm)

Figure 4



3.5
3
2.5
2
1.5
1
0.5
0
average number of saccades
upper quartile, first saccade-touch distance
lower quartile, first saccade-touch distance
penalty disk (red)
target disk (green)
open loop
background luminance

Figure 5



250
200
150
100
50
0
number of events
−180
−135
−90
−45
0
45
90
135
180
direction of second saccade (°)
initial eye position
direction of
second
saccade
first
saccade
touch point
second
saccade

Figure 6

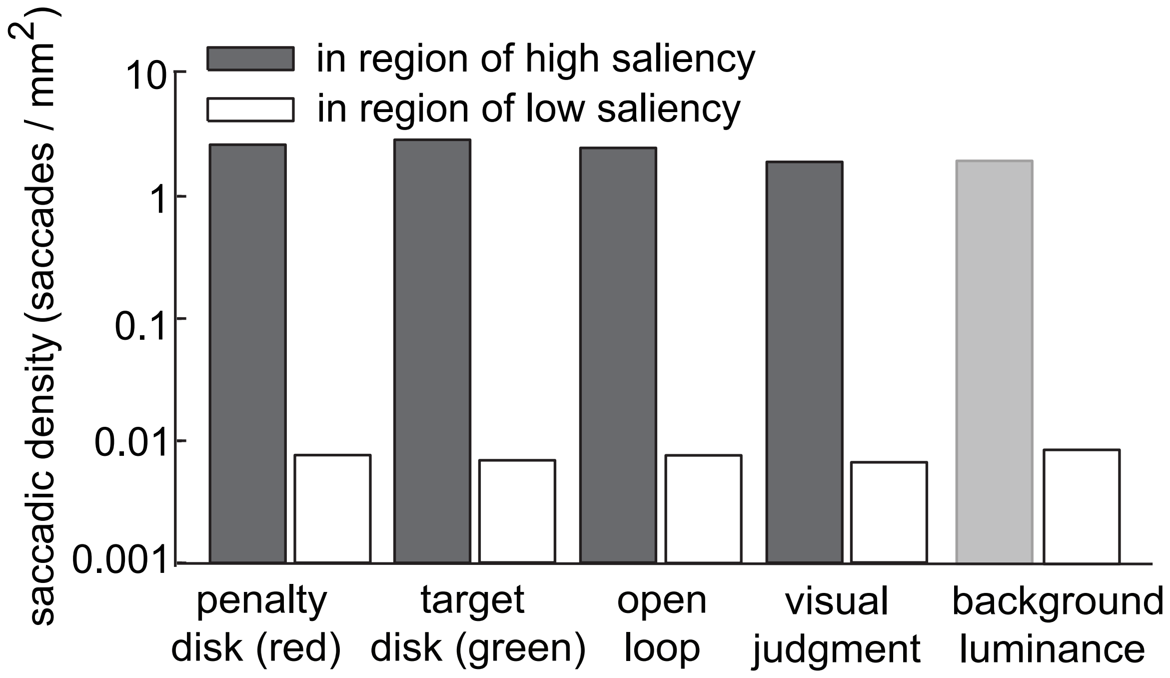
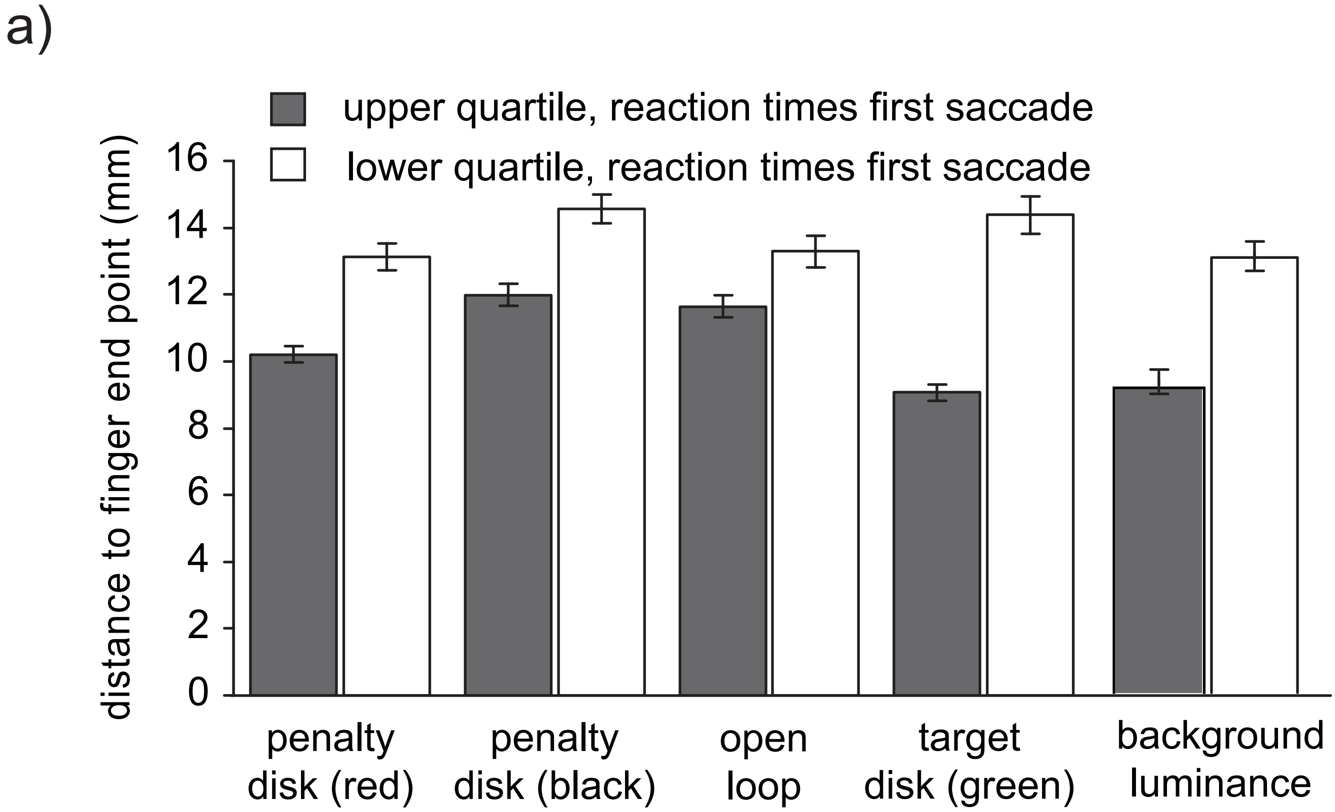

saccadic density (saccades / mm^2)
in region of high saliency
in region of low saliency
10
1
0.1
0.01
0.001
penalty disk (red)
target disk (green)
open loop
visual judgment
background luminance

Figure 7


a)
upper quartile, reaction times first saccade
lower quartile, reaction times first saccade
distance to finger end point (mm)
0
2
4
6
8
10
12
14
16
penalty disk (red)
penalty disk (black)
open loop
target disk (green)
background luminance

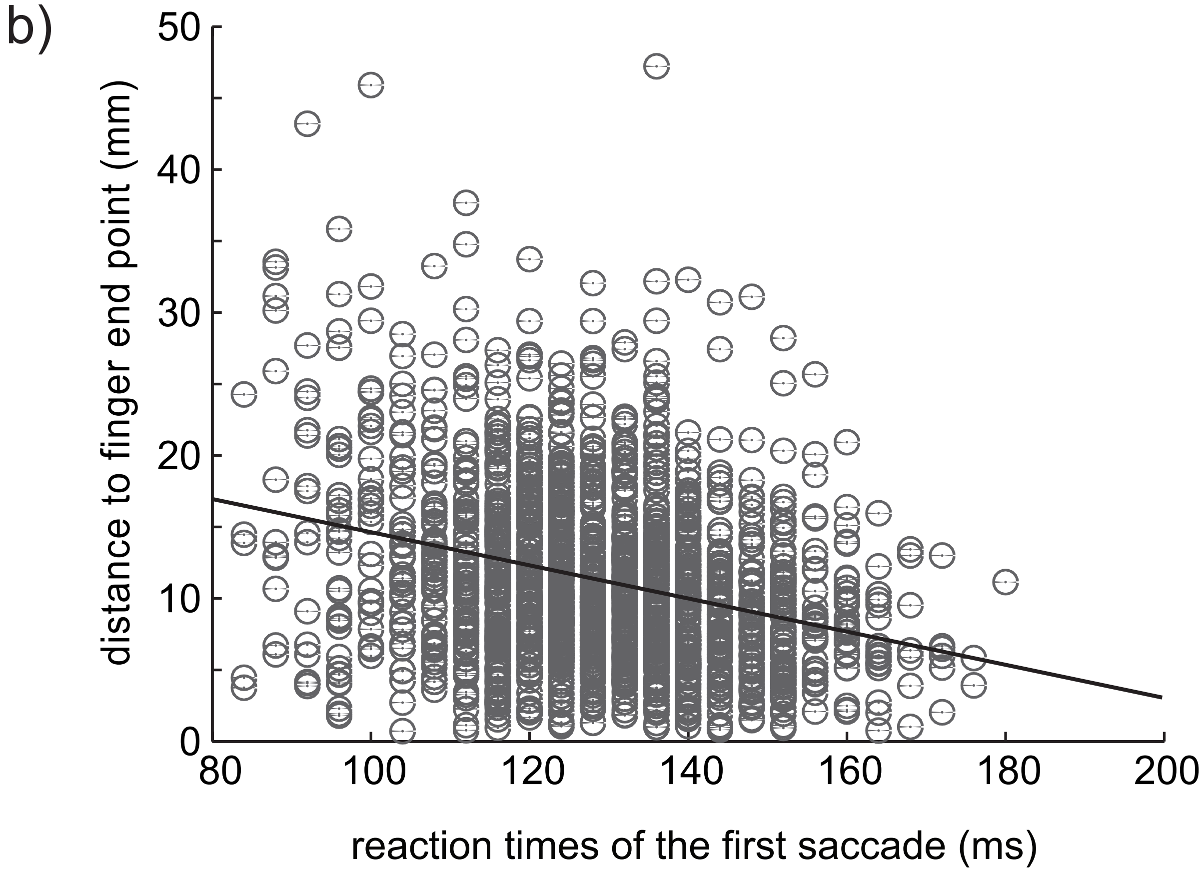

b)
distance to finger end point (mm)
0
10
20
30
40
50
80
100
120
140
160
180
200
reaction times of the first saccade (ms)

Figure 8

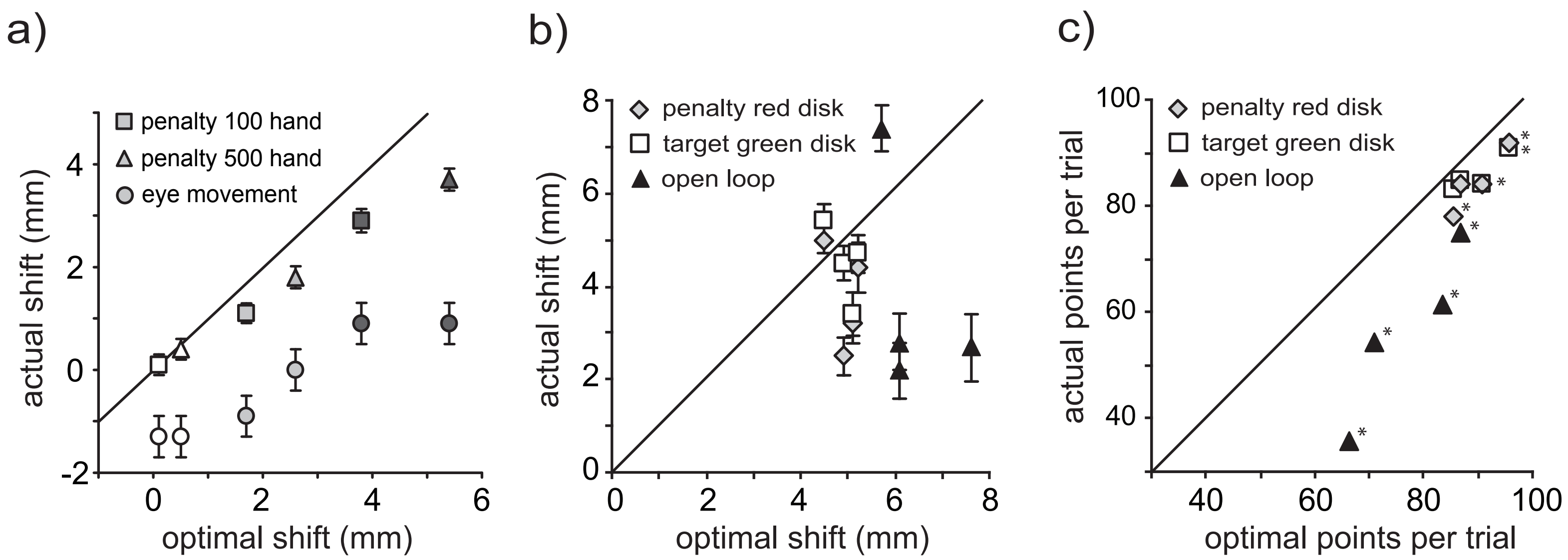

a)
penalty 100 hand
penalty 500 hand
eye movement
actual shift (mm)
optimal shift (mm)
b)
penalty red disk
target green disk
open loop
actual shift (mm)
optimal shift (mm)
c)
penalty red disk
target green disk
open loop
actual points per trial
optimal points per trial

Figure 9