Optimality of saccadic eye movements under risk

Martin Stritzke\(^1\), Julia Trommershäuser & Karl R. Gegenfurtner

Giessen University, Department of Psychology,
Otto-Behaghel-Str. 10F
35394 Giessen, Germany

\(^1\): Author to whom correspondence should be addressed:
Martin Stritzke
Department of Psychology
Otto-Behaghel-Str. 10F
35394 Giessen, Germany
Email: martin.stritzke@psychol.uni-giessen.de
Phone: +49 641 99 26113, Fax: +49 641 99 26119

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Abstract

It has been shown that humans select visuo-motor strategies maximizing gain during speeded hand movements under risk. Here we studied saccadic eye movements in a task in which we provided monetary rewards and losses depending on the endpoint of the saccade. Saccades into a color coded target region won points; saccades into a partially overlapping or abutting penalty region could yield a loss. Participants were instructed to maximize their gain by winning as many points as possible. We compared participants’ scores to the score of an optimal observer which was calculated based on each participant’s saccadic endpoint variability, similar to a recent model of optimal movement planning under risk (Trommershäuser et al., 2003b). We employed 3 different experimental paradigms (‘Gap’, ‘No Gap’ and ‘Overlap’) to manipulate saccadic latencies and an experiment with a longer delay period (‘Memory’). Scores in the ‘Gap’ experiment were poor in trials with the shortest latencies (120-140 ms), but improved significantly with longer latencies. Compared to the ‘Gap’ experiment, latencies were on average 20 ms longer in the ‘No Gap’ experiment and 55 ms longer in the ‘Overlap’ experiment. Scores remained largely unaffected by the paradigm for latencies larger than 160 ms. This shows that processing of reward related information does not interfere with other processes that occur before the eye starts moving (e.g. disengaging of fixation, preparatory eye movements). We conclude that, with additional time of approximately 35 ms for processing of stimulus information (color-coding of reward information), saccades can be planned and executed optimally.
Introduction

Saccadic eye movements are a fundamental and inherent feature of human foveated vision and have been studied extensively for more than a century (Javal, 1878; Dodge, 1903). Saccadic eye movements allow us to foveate targets at different locations in the visual field in close temporal succession. By now, saccadic eye movements have been characterized in great detail (Carpenter, 1988). Recently, saccadic eye movements have been used as an appropriate and convenient way to explore motor performance that is controlled by sensory processing (e.g. Najemnik & Geisler, 2005; White et al., 2008). In the last decades, the notion of optimal sensori-motor behavior on the one hand, and the computation of attributes like reward, value or gain in a sensori-motor task on the other hand, have emerged as two relevant issues of significant impact (see e.g. Glimcher, 2001; Platt & Glimcher, 1999; Schultz, 2006; Sugrue et al. 2005).

Information for 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) towards supplementary eye fields (SEF), frontal eye fields (FEF), areas in the parietal cortex lateral, most prominently intraparietal area (LIP) and SC. Both FEF and SC are believed to play an important role for the goal selection and preparation of saccadic eye movements (Munoz, 2002; Krauzlis et al., 2004).

When preparing an eye movement, several processes take place, such as shift of the visual attention to the new target, disengagement of oculomotor fixation, and computation of the movement parameters (see e.g. Findlay & Walker 1999). There is evidence that the time needed to prepare for 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 (1967), who varied the point in time of fixation stimulus offset relative to target onset. The reliable finding of shorter latencies in the gap
paradigm could be due to facilitation of the disengagement of fixation and attention (Ross & Ross, 1980; Kingstone & Klein 1993). Ross and Ross (1980) argued that the gap effect consists of two components, a warning signal effect and a second effect which has been called fixation release or fixation disengagement.

**Processing of Reward Related Information**

Area LIP has been shown to increase neuronal activity in relation to saccadic eye movements in general (Colby et al., 1996) and might be involved in the allocation of spatial attention and motor intention (see, e.g., Andersen & Buneo, 2002; Colby & Goldberg, 1999; Bisley & Goldberg, 2003). Furthermore, neurons in LIP are believed to be responsible for the encoding of attributes like reward, gain or value (Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Sugrue et al., 2004). Platt and Glimcher (1999), for instance, argue that humans and animals decide what to do in a given situation by assessing the relative value of each possible response. 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 (Platt & Glimcher, 1999). In a similar study, Sugrue and colleagues (2004) 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 remapping abstract valuation to concrete action rather than directly computing attributes like reward or value (Sugrue et al., 2004). Similarly, Roitman and Shadlen (2002) concluded that activity of LIP neurons is predictive for the monkey’s decision in a combined motion-discrimination reaction-time task (Roitman & Shadlen, 2002).

Besides the question where and how reward might be coded in the brain, a separate question concerns the time course of reward information processing. Milstein & Dorris (2007)
demonstrated that saccadic reaction times (SRTs) correlated negatively with relative expected value. In addition, SRTs correlated higher with the relative expected value than with parameters like reward probability or reward magnitude alone (Milstein & Dorris, 2007). A neurophysiology study has shown that neurons in the monkey parietal cortex show increasing task-related activity with both the reward magnitude and reward probability but do not seem to distinguish between the two components (Musallam et al., 2004). However, due to the presence of neural noise it remains difficult to determine exactly whether neurons encode a certain attribute like expected value. In all these studies (Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Sugrue et al., 2004; Milstein & Dorris, 2007) saccadic eye movements were used as an indicator for a decision process which could have also been achieved by a button press in a similar way. In our study, we explored the fine tuning of the saccadic system by directly linking the exact endpoint of the saccade to a reward or a loss.

**Bottom-Up vs. Top-Down Attributes**

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 (Itti & Koch, 2000, 2001) or the luminance defined center-of-gravity of a stimulus configuration (e.g. Whitaker et al., 1996; Vishwanath et al., 2000). However, recent studies have argued that saliency cannot fully account for all aspects of human gaze behavior (e.g. Tatler, 2007) and have emphasized the importance of the task at hand as a crucial determinant (e.g. Rothkopf et al., 2007; Einhäüser et al., 2008).

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 a rapid pointing task under risk (Stritzke & Trommershäuser, 2007). 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 towards 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 towards the finger endpoint.

Here we report the results of a study in which 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 (100 points per trial), saccadic responses into the penalty region could incur a loss (500 points per trial). Scores for each participant were compared to 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 movement planning under risk (Trommershäuser et al., 2003a,b), see Methods for details. The experiments of Trommershäuser et al. demonstrated that, during speeded hand movements under risk, participants selected strategies which came very close to optimal behavior maximizing expected gain. Here, we asked whether saccadic eye movements follow the same principles of processing of reward related information as hand movements under risk. We employed 3 different experimental paradigms (‘Gap’, ‘No Gap’ and ‘Overlap’) to manipulate saccadic latencies, as well as an experiment requiring a memory guided saccade (‘Memory’).

**Methods**

**Equipment**

Participants performed the experiments in a dimly lit room in front of a 21-inch computer monitor (ELO ET2125C, resolution 1280 x 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).

**Stimuli**

Stimuli consisted of a target circle and a penalty circle and were presented on a gray background (luminance: 33 cd/m²). 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/m² and the filled green circle had a luminance of 67 cd/m². This resulted in a contrast of 0.34 for a green or red filled circle compared to the gray background.

Stimuli were presented unpredictably at a random position, within an annulus of 4-6° eccentric from initial fixation at screen center. Both 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 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 (Figure 1). The spatial position of stimulus presentation 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).

**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.

Experiment 3 (‘Overlap’): After the button press and a variable delay of 400-700 ms, 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 also Figure 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. Participants never received spatial feedback about the landing point of their first saccade. 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 to 4 and 9 to 12, penalty value 500 in blocks 5 to 8 and 13 to 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 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 sixteen blocks of forty trials each. Each block of trials consisted of 8 repetitions of each of the four spatial stimulus configurations and eight control trials, presented in random order. Participants needed approximately 60-70 minutes 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°). Participants were instructed to look at the target as quickly and accurately as possible and win as many points as possible. Data collection was carried out over several sessions conducted on different days. The order of conditions within an experiment was randomized across participants.

Participants

6 participants participated in this study, all 6 took part in experiment 1, all except KB and NH took part in experiments 2, 3 and 4. The participants were 5 female psychology 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 unaware of the hypotheses under test. Participants were informed of the payoffs and penalties for each block of trials. All participants had given their informed consent prior to testing and 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 5000 points in addition to the fixed amount of 8 € per hour.

**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 x-direction between the target center and the final saccadic position 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 saccadic endpoint positions generated by the *Eyelink II* software were used to calculate the feedback that was presented after each trial. Further 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 were excluded from data analysis.

Saccadic endpoints were analyzed with respect to endpoint variability and relative distance in x-direction from the target center. Trials were sorted by saccadic latency in
ascending order and divided into sextiles (quantiles of six equal proportions). When comparing participants’ scores to the optimal scores maximizing gain, we analyzed trials with a penalty value of 500 and trials with a penalty value of 0 separately.

**Optimal Performance**

Participants’ performance in terms of gain or loss was compared to a model of optimal movement planning based on each participant’s measured saccadic endpoint variability. This model uses measured endpoint variability as an estimate for each participant’s motor variability and predicts maximum expected gain depending on target and penalty value, size and spatial configuration (for more details see Trommershäuser et al. 2003a,b, Stritzke & Trommershäuser 2007). Participants’ endpoint variability was estimated from the distribution of saccadic endpoints in the control trials (presentation of target circle only) for each participant and each experiment, averaged across saliency conditions. We computed separate estimates of variability in x-direction and y-direction for each participant and each experiment.

The saccadic latency in conditions in which optimal performance occurred was compared to the latency value of the (lowest) 5\textsuperscript{th} percentile of the latency distribution in this condition. This was conducted to exclude the fastest responses in each condition from the computation of additional time for reward processing information.

**Model of Optimal Saccadic Movement Planning**

Participants’ saccadic responses were compared to a model of optimal saccadic movement planning. Similar as in a recent model of optimal movement planning for rapid pointing under risk (Trommershäuser et al., 2003a,b), 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 and the participant’s own task-relevant saccadic endpoint variability. For the conditions of our experiment, the expected gain of motor strategy $S$ is defined by

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

(1)

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

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

(2)

Once participants were practiced in the task, variability in $y$-direction (direction of the saccade) was slightly higher than variability in $x$-direction (as typically found in similar tasks, e.g. van Opstal & van Gisbergen, 1989; van Beers, 2007) and remained constant throughout the experiment (i.e., independent of spatial and penalty conditions). The probability of hitting region $R_i$ is then defined by the choice of $(x, y)$ on the screen and the participant’s endpoint variability $\sigma = (\sigma_x, \sigma_y)$ as

$$P(R_i | \bar{x}, \bar{y}, \sigma_x, \sigma_y) = \int_{R_i} p(x, y | \bar{x}, \bar{y}, \sigma_x, \sigma_y) \, dx \, dy.$$  

(3)

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

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

(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 endpoint position is the
center of the target region. For non-zero 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 $\sigma$.

**Results**

*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 in the ‘Gap’ experiment and the ‘Overlap’ experiment. Saccades with the shortest latencies in the ‘Gap’ experiment exhibited an undershoot of about 1° 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 landed in the center region of the target. In the ‘No Gap’ experiment, saccades with the shortest latencies exhibited only a tiny undershoot but landed between the vertical symmetry axis of the target / penalty configuration and the target center. Saccades with the longest latencies in the ‘No Gap’ experiment landed 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 circle, but undershot the center of the circle by an amount of 0.75° on average with a tendency of increasing undershoot with longer latencies (Figure 3).

To investigate the effects of spatial condition (‘near’ vs. ‘far’) and penalty value (penalty 0 vs. penalty 500) on shift of saccadic endpoints away from the penalty region, we conducted a 3-way ANOVA with factors experiment, spatial condition and penalty value for all participants. We observed a significant main effect of ‘experiment’ ($p < 0.001$ for all participants) and spatial condition on shift of saccadic endpoints 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) and we observed a significant main effect of penalty value on shift of saccadic endpoints for 3 out of 4 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, the magnitude of the shift turned out to be much smaller than predicted for an optimal participant maximizing gain (as defined by Eq. 4) in all experiments. There was no significant interaction of spatial condition and penalty value.

As expected, the distributions of saccadic latencies were significantly different 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).

**Hits, Score and Distance to the Target**

In direct consequence 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 Figure 4, 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 at 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 slightly decreased with longer saccadic latency. In the ‘Gap’, ‘No Gap’ and ‘Overlap’ experiments, a small effect of stimulus saliency (‘target filled’ vs. ‘circles’ vs. ‘penalty filled’) was observed (‘target filled’ vs. ‘circles’ vs. ‘penalty filled’, see also Figure 4). The percentage of hits into the target region in fast trials was significantly lower than the percentage of hits in slow trials for 3 out of 4 participants in the ‘Gap’ experiment ($\chi^2$-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 ($\chi^2$-test: $\chi^2_1 =$
9.05, p < 0.01; χ² = 17.6, p < 0.001; χ² = 17.8, p < 0.001) and in the ‘Overlap’ experiment (χ²-test: χ² = 8.76, p < 0.01; χ² = 0.69, p = 0.41; χ² = 27.6, p < 0.001; χ² = 30.0, p < 0.001). This was not the case in the ‘Memory’ experiment (χ²-test: p > 0.05 for all participants). All participants reached a higher score when the target circle was filled compared to when the penalty circle was filled in the ‘Gap’ experiment (χ²-test: χ² = 7.65, p = 0.05; χ²-test: χ² = 4.60, p = 0.20; χ²-test: χ² = 62.5, p < 0.001; χ²-test: χ² = 15.4, p < 0.01) and in the ‘No Gap’ experiment (χ²-test: χ² = 12.5, p < 0.01; χ²-test: χ² = 5.91, p = 0.12; χ²-test: χ² = 100.6, p < 0.001; χ²-test: χ² = 12.3, p < 0.01). All participants except participant 3 reached a higher score when the target circle was filled in the ‘Overlap’ experiment (χ²-test: χ² = 6.98, p = 0.07; χ²-test: χ² = 83.9, p < 0.001; χ²-test: χ² = 6.89, p = 0.07) and in the ‘Memory’ experiment (χ²-test: χ² = 51.3, p < 0.001; χ²-test: χ² = 118.6, p < 0.001; χ²-test: χ² = 9.77, p < 0.05). As can be seen, however, these observations did not always turn out to be significant.

In the ‘Gap’ experiment, the distance between saccadic endpoint and target center decreased from about 11 mm for trials with the shortest latencies to about 8 mm for trials with the longest latencies (Figure 5). In the ‘No Gap’ experiment, the distance decreased from about 7.5 mm for trials with the shortest latencies to about 7 mm for trials with the longest latencies, in the ‘Overlap’ experiment, the distance decreased from about 7 mm to about 6 mm. In the ‘Memory’ experiment, no correlation was observed between saccadic latency and the change in distance from saccadic endpoint to the target center; the distance remained constant at about 10 mm on average. Thus, apart from trials with very short saccadic latencies in the ‘Gap’ experiment, the distance from saccadic endpoint to the target center was very similar in the ‘Gap’, ‘No Gap’ and ‘Overlap’ experiments.

In order to investigate the effects of spatial condition (‘near’ vs. ‘far’) and penalty value (penalty 0 vs. penalty 500) on the distance of saccadic endpoints to the target center, we conducted a 3-way ANOVA with factors experiment, spatial condition and penalty value for
all participants. While we observed a significant main effect of spatial condition on distance to the target center in 3 out of 4 participants ($F(1,5309) = 0.14, p = 0.71$; $F(1,5739) = 6.73, p < 0.01$; $F(1,5739) = 18.4, p < 0.001$; $F(1,5958) = 52.2, p < 0.001$), we did not observe a significant main effect of penalty value on distance to the target center ($p > 0.05$ for all participants).

**Optimal Saccadic Performance**

As shown in Figure 6, performance improved with longer saccadic latencies in the ‘Gap’, ‘No Gap’ and ‘Overlap’ experiments, but did not change in the ‘Memory’ experiment. However, optimal performance maximizing expected gain was never entirely reached, but ranged between 80% and 100% of optimal performance in the ‘Gap’, ‘No Gap’ and ‘Overlap’ experiments (data pooled across participants). Again, saccades with the shortest latencies in the ‘Gap’ experiment mark an exception here, with performance reaching only about 40% - 55% of optimal performance maximizing gain. In the ‘Memory’ experiment, performance reached about 80% of optimal performance and did not change substantially 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. Comparing the data across participants and conditions, we find that optimal performance was reached in 52 out of 216 conditions. 216 conditions resulted from the ‘Gap’ experiment completed by 6 participants in 3 saliency conditions, 2 penalty conditions and 2 spatial conditions and the ‘No Gap’, ‘Overlap’ and ‘Memory’ experiments completed by 4 participants in 3 saliency conditions, 2 penalty conditions and 2 spatial conditions. Optimal performance occurred more frequently in the ‘Overlap’ (19 out of 48) and ‘Memory’ (19 out of 48) experiments than in the ‘Gap’ (9 out of 72) and ‘No Gap’ (5 out of 48) experiments. Moreover, optimal performance occurred more frequently in penalty 0 conditions (36 vs. 16 in penalty 500 trials) and in near spatial conditions (29 vs. 23 in the far spatial conditions).
Finally, optimal performance occurred more frequently when the target circle was filled (26 vs. 15 in the circles conditions and 11 in the penalty filled conditions). Figure 7 shows data from only those conditions in which we observed optimal performance. Data points represent the latency values of optimal performance as a function of the value of the 5th percentile of the latency distribution in the corresponding condition. Data points from the ‘Memory’ experiment are spread out across a wide range of latency values whereas data points from the other three experiments cluster within a more narrow range. The three data points which indicate the fastest latencies from the ‘Memory’ experiment derive from a participant who seemed to reliably anticipate the end of the memory interval. This led to surprisingly short latencies in some conditions. The average across all displayed conditions shows that participants need additional time of approximately 35 ms to plan their saccadic response in an optimal fashion (see Figure 7).

**Comparison across Experiments**

In the ‘Memory’ experiment, the distribution of saccadic endpoints did not change significantly with increasing saccadic latency. Accordingly, the frequency of hits in the target and penalty circles, the distance from the saccadic endpoints to the target center and the performance in terms of score and percentage of optimal performance reached did not depend on saccadic latency either. In the other three experiments, especially the ‘Gap’ experiment, however, participants’ performance did depend on saccadic latency. Interestingly, scores at a given latency level were very similar in all three experimental paradigms. For instance, scores within the latency range of 160 - 200 ms were not significantly different across experiments in penalty 0 trials ($\chi^2$-test: $p > 0.05$ for all participants) and penalty 500 trials ($\chi^2$-test: $p > 0.05$ for all participants, see also Figure 6).

**Discussion**
In a series of four experiments, we studied contributions of top-down and bottom-up features during saccadic eye movements under risk. Our participants performed saccadic eye movements whose outcomes were directly associated with a reward or a possible loss. With the exception of the ‘Memory’ experiment, participants’ performance, i.e. the percentage of hits into the target region and points won, varied systematically with the latency of the saccadic response. In the conditions in which optimal performance (as predicted for a subject maximizing gain) was reached, additional time of approximately 35 ms for processing compared to the 5th percentile of the respective latency distribution was necessary. Furthermore, a higher saliency of the target region and a low penalty value facilitated the achievement of optimal performance. Scores at a given latency level in experiments ‘Gap’, ‘No Gap’ and ‘Overlap’ remained largely unaffected by the experimental paradigm.

**Saccades vs. Pointing**

We first discuss why visuo-motor strategies during rapid pointing under risk (Trommershäuser et al., 2003a,b, 2005, 2006) are closer to optimal behaviour maximizing gain 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. Saunders & Knill, 2004). Visual feedback during the movement allows for movement corrections and enhances motor performance (e.g. Chua & Elliott, 1993). 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. Panchuk & Vickers, 2006; Land & McLeod, 2000). 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 to bring the target into focus. If the first saccade ends not exactly on the desired spot, a second, corrective saccade is made to finally get there. This happens very rapidly and usually without any disadvantages for the performance in a natural task, also due to the fact that eye movements are usually faster than pointing movements (see e.g. Binsted et al., 2001; Gribble et al., 2002). In addition, it has been shown that making a saccade can be rather economic and preferable compared to fully utilizing visual short-time memory capacity in a visual short-term memory task (Droll & Hayhoe, 2007) which could be regarded as an indicator that making a saccade is relatively ‘cheap’ and requires only little effort.

**Contribution of Bottom-Up and Top-Down Factors**

The results of our study can be explained by two parallel processes: 1) stimulus localization (rapid processing of stimulus features like color/contrast/shape with peripheral vision) and 2) finding the optimal endpoint based on computing maximum expected gain. In other words, 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 (e.g. Whitaker et al., 1996; Vishwanath et al., 2000) or visual saliency of the stimulus (Itti & Koch, 2000). 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. Rothkopf et al., 2007; Einhäuser et al., 2008). 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.

**Processing of Reward and Optimality**

There is an important difference between our study and the electrophysiological approaches described above (Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Sugrue et al., 2004; Milstein & Dorris, 2007). These studies used the saccadic eye movement as an indicator for a decision process in the presence of color coded reward information which 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 vs. to the left.

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. Depending on the saliency of the target region and the magnitude of the penalty value, additional time of approximately 35 ms is needed to plan and execute eye movements optimally in the presence of rewards and losses. 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 gain in other conditions. We speculate that this time is needed to reliably
recognize the target and to process the information about possible reward or loss and is just not available in trials with very short latencies.

As expected, the use of different experimental paradigms (‘Gap’, ‘No Gap’ and ‘Overlap’) led to different latency distributions. Performance at a given latency level, however, remained largely unaffected by the experimental paradigm. This shows that the time needed to e.g. disengage fixation does not influence the goal selection for saccadic eye movement and that attentional processes and target selection can occur in parallel.
References


Figure captions:

Figure 1: Stimulus configuration. Stimuli were presented randomly within an annulus 4° - 6° eccentric from initial fixation which was in the center of the screen. The circles were presented adjacent to each other or overlapped by 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.

Figure 2: Trial procedure. The display of a fixation cross at screen center indicated the start of the trial in all 4 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.

Figure 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 brown dots indicate saccadic endpoints from the sextile with shortest latencies; the blue dots indicate saccadic endpoints from the sextile with longest latencies. Circles denote the mean of a sextile. The large green circle denotes the target area; the large red 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’).
Figure 4: **Target and penalty hit frequency.** Percentage of hits into the target (green), penalty (red) and background area (black) 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.

Figure 5: **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.

Figure 6: **Comparison of efficiency across experiments.** Comparison of efficiency (actual scores divided by optimal scores) for all experiments 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.

Figure 7: **Saccadic latency at optimal performance.** Latency values of conditions in which optimal performance is reached as a function of latency values at the 5th percentile of the
latency distribution in the respective condition. Different symbols denote different experiments, different colors correspond to individual participants.
'Gap' Exp. 1

* Saccade endpoint

Stimulus onset

Gap 200 ms

Button press

'No Gap' Exp. 2

* Saccade endpoint

Stimulus onset

300 - 700 ms

Button press

'Overlap' Exp. 3

* Saccade endpoint

Stimulus onset

300 - 700 ms

Button press

'Memory' Exp. 4

* Saccade endpoint

Memory 500 ms

Stimulus 100 ms

300 - 700 ms

Button press

Time