

Earlier saccades to task-relevant targets irrespective of relative gain between peripheral and foveal information

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Saccades bring objects of interest onto the fovea for high-acuity processing. Saccades to rewarded targets show shorter latencies that correlate negatively with expected motivational value. Shorter latencies are also observed when the saccade target is relevant for a perceptual discrimination task. Here we tested whether saccade preparation is equally influenced by informational value as it is by motivational value. We defined informational value as the probability that information is task-relevant times the ratio between postsaccadic foveal and presaccadic peripheral discriminability. Using a gaze-contingent display, we independently manipulated peripheral and foveal discriminability of the saccade target. Latencies of saccades with perceptual task were reduced by 36 ms in general, but they were not modulated by the information saccades provide (Experiments 1 and 2). However, latencies showed a clear negative linear correlation with the probability that the target is task-relevant (Experiment 3). We replicated that the facilitation by a perceptual task is spatially specific and not due to generally heightened arousal (Experiment 4). Finally, the facilitation only emerged when the perceptual task is in the visual but not in the auditory modality (Experiment 5). Taken together, these results suggest that saccade latencies are not equally modulated by informational value as by motivational value. The facilitation by a perceptual task only arises when task-relevant visual information is foveated, irrespective of whether the foveation is useful or not.

Introduction

The human visual system comprises a large field of view with only a small and central region, the fovea, ensuring high visual acuity. In contrast to foveal vision, visual acuity in the periphery is comparatively poor. As a consequence, the fovea has to be oriented toward objects of interest to obtain detailed visual information. This is achieved by fast eye movements called saccades. The time it takes the eye to respond to an upcoming target (i.e., the latency), as well as other saccade dynamics (such as peak velocity) can be used to infer characteristics of visual processing and oculomotor control.

Eye movements are not only influenced by bottom-up factors like target contrast and color, but also by top-down factors like motivation (i.e., the desire to perform a particular action or achieve a certain outcome) and plans (e.g., Schütz, Lossin, & Gegenfurtner, 2015; Schütz, Trommershäuser, & Gegenfurtner, 2012; for reviews, see Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Schütz, Braun, & Gegenfurtner, 2011; Tatler, Hayhoe, Land, & Ballard, 2011). Saccades to rewarded targets show reduced latencies (Milstein & Dorris, 2007, 2011; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002) and increased peak velocities (Chen, Hung, Quinet, & Kosek, 2013; Takikawa et al., 2002). Milstein and Dorris (2007) found that saccade latencies to single targets are negatively correlated with the expected value (i.e., reward magnitude \times reward probability) of a saccade target, and this correlation was stronger than a correlation with reward magnitude or reward probability only. In total, latencies to targets with high expected value were reduced by approxi-

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mately 40 ms compared to targets of low value. Milstein and Dorris (2007) concluded that expected motivational value is represented in oculomotor areas and influences the preparation of saccades. Motivation by reward can increase response speed without reducing accuracy, and thus can help to overcome the speed–accuracy trade-off (Manohar et al., 2015). A representation of expected value would thus be beneficial to speed up responses to rewarded targets and obtain rewards earlier without giving away accuracy. However, it can be argued that receiving a monetary reward for an eye movement is an artificial scenario, as eye movements naturally do not provide rewards but provide visual information about our environment.

The same benefit in eye movement latency of close to 40 ms and increased peak velocities can be observed when saccades are initiated in order to obtain information for a perceptual task (task-related saccade) compared to saccades that are merely elicited to fixate a target (target-elicited saccade) without the requirement for further information processing (Bieg, Bresciani, Bühlhoff, & Chuang, 2012; Guyader, Malsert, & Marendaz, 2010; Montagnini & Chelazzi, 2005; Trotter & Pratt, 2005). Montagnini and Chelazzi (2005) had their participants saccade to briefly presented targets and suggested that this benefit arose because the target was only presented briefly and perception would benefit from an early saccade. Bieg et al. (2012) showed that the effect persists if the target is displayed for longer durations, ruling out the urgency explanation. They suspected that the difference between task-related and target-elicited saccades might be related to motivational factors and that both saccade types are affected differently by repetitions. Another possibility that can explain the difference between task-related and mere target-elicited saccades is that the brain assigns a value to the information that can be obtained by executing the saccade, and that the preparation of saccades is modulated by this informational value in the same way as it is modulated by motivational value (Milstein & Dorris, 2007). This representation of informational value would help to obtain task-relevant information earlier and might affect the speed–accuracy trade-off in the same way as motivation by reward (Manohar et al., 2015).

To solve a perceptual task, we need to gather task-relevant information. The amount of information provided by a saccade depends on the target discriminability after the eye movement compared to target discriminability before the eye movement. For a saccade target, this corresponds to the relation between foveal and peripheral discriminability. Evidence that the oculomotor system utilizes information about the discriminability across the retina comes from optimal statistical models of eye movement planning (Najemnik

& Geisler, 2005; Peterson & Eckstein, 2012; Renninger, Vergheze, & Coughlan, 2007). These models assume that the visual system has information about its own sensitivity across the retina and optimizes information gain given its own constraints. However, these studies manipulated informational value indirectly and did not directly test whether the expected informational value is used in saccade preparation.

The aim of the current study was to investigate whether saccade latencies are modulated by the task-relevant information that can be obtained by saccade execution. If so, this would suggest that there is a representation of informational value, which can be used for the preparation of saccades. Moreover, it could explain the differences between mere target-elicited saccades and task-related saccades that are executed in order to sample task-relevant information. We define informational value, $value_{inf}$, as the product of information gain, $gain_{inf}$, and the probability that this information is task-relevant, p_{task} :

$$value_{inf} = gain_{inf} \times p_{task} \quad (1)$$

with the gain in information for a saccade being the ratio between postsaccadic foveal and presaccadic peripheral discriminability:

$$gain_{inf} = \frac{discriminability_{fovea}}{discriminability_{periphery}} \quad (2)$$

As a consequence of Equation 1, targets only carry informational value if they are task-relevant ($p_{task} > 0$). For any task-relevant target, the informational value increases with the gain in information, $gain_{inf}$. Whereas this information gain usually depends on the visual sensitivity across the retina, we here used a gaze-contingent display to independently manipulate foveal and peripheral discriminability and thus the gain in information a saccade provides (Experiments 1 and 2). In Experiment 3, we varied the task-relevance, p_{task} , while keeping the information gain, $gain_{inf}$, constant. In two further experiments, we confirmed that the difference between task-related and target-elicited saccades is spatially specific and not due to generally heightened arousal (Experiment 4) and we showed that the difference between the two saccade types does not emerge when the perceptual task is not in the visual but in the auditory modality (Experiment 5).

Experiment 1: Manipulating information gain

If we saccade to any target that is relevant for a (perceptual) task, the execution of the saccade will lead to a gain in visual information, because spatial

resolution and sensitivity is usually superior in the fovea than in the periphery. In this experiment, participants had to saccade to a plaid stimulus and judge the orientation of its vertical component. We independently manipulated peripheral and foveal discriminability relative to previously determined individual thresholds. Both peripheral and foveal discriminability could be either above or below threshold, independently of each other. If saccades are influenced by the informational value for a perceptual task, then we would expect shorter saccade latencies when participants can gain information (periphery: below; fovea: above, B–A) compared to conditions where participants do not gain information, because peripheral and foveal discriminability are either both above or below threshold (A–A, B–B). Moreover, we would expect prolonged latencies (or even that participants do not execute saccades) when they lose information by making an eye movement; thus, when the foveal discriminability of the target is worse than the peripheral one (above to below, A–B). Individual discrimination thresholds in the fovea and the periphery were initially assessed during fixation (fixation task). Saccade latencies were then assessed without a perceptual task (saccade-only task) and with a perceptual task under different discriminability conditions (perceptual saccade task).

Methods

Participants

Observers were 19 undergraduate students from Giessen University. All observers were paid for participation (8 €/h) and had normal or corrected-to-normal vision. All experiments reported in this study were conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and were approved by the local ethics committee, LEK FB06, at Giessen University (proposal number 2013-0020). All observers gave informed consent prior to participation. Three participants were dismissed after completing the fixation task because their psychometric functions did not reach 90% performance. Thus, for the perceptual saccade task, we have a complete data set for 16 participants (mean age = 24.9 years; range: 19–31 years; 13 women, three men). Twelve of them (and one of the three discarded participants) had previously participated in the saccade-only task.

Apparatus and stimuli

Stimuli were displayed using the Psychtoolbox (Brainard, 1997) in MATLAB (MathWorks, Inc., Natick, MA). For the first three participants, stimuli were displayed on a 21-in. SONY GDM-F520 CRT

monitor with a refresh rate of 100 Hz. The monitor had a size of 37×29.6 cm, a spatial resolution of 1280×1024 pixel and was placed at 47 cm distance. For the remaining 13 participants, stimuli were displayed on a VIEWPixx monitor (VPixx Technologies, Saint-Bruno, QC, Canada) with a refresh rate of 120 Hz at a viewing distance of 48.5 cm. It had a spatial resolution of 1920×1080 pixel and a size of 51.5×29 cm. Eye movements of the right eye were recorded using the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002) and a tower-mounted EyeLink 1000 (SR Research Ltd., Ottawa, ON, Canada) with a sampling rate of 1000 Hz. Participant responses were recorded via a standard keyboard. As fixation cross, we used a combination of a bullseye and a crosshair with an outer diameter of 0.6° (Thaler, Schütz, Goodale, & Gegenfurtner, 2013).

Stimuli were plaids (i.e., sums of a vertical and horizontal grating), each with a spatial frequency of $SF = 2$ cycles per degree seen through a Gaussian window with a standard deviation of 0.4° of visual angle. Whereas the horizontal component was perfectly aligned to the cardinal axis, the vertical component was tilted clockwise (cw) or counterclockwise (ccw) by 10° . As changing the contrast of a Gabor patch influences its saliency and also its perceived size (Fredericksen, Bex, & Verstraten, 1997), we instead used a plaid and only varied the contrast ratio of both gratings while keeping the overall contrast constant. This allowed us to manipulate the discriminability of the task-relevant vertical component, without affecting saccade latencies via saliency. Contrasts of both patches added up to a fixed Michelson contrast of $C = 0.4$. For instance, a vertical contrast of 0.1 means that the horizontal contrast was 0.3. Hereafter, we report the contrast of the vertical component only. For the saccade-only task, vertical contrasts varied logarithmically in five discrete steps from 0.04 to 0.16. Contrast values in the perceptual saccade task were retrieved relative to individual psychophysical thresholds.

Fixation task to determine individual thresholds

In the fixation task, plaid stimuli had a vertical contrast that varied in nine logarithmically spaced steps from 0.008 to 0.2 for the fovea, and from 0.028 to 0.25 for the periphery (method of constant stimuli). At the beginning of each trial, a centrally appearing fixation-cross signaled participants they could start a trial by pushing the space bar. After a random time of 750 to 1500 ms, the plaid appeared at the screen center replacing the fixation cross or at a horizontal eccentricity of 12.5° (left or right), in which case the fixation cross remained visible. Participants had to maintain fixation at the screen center. The plaid remained visible for 400 ms. A bar appeared that was randomly tilted

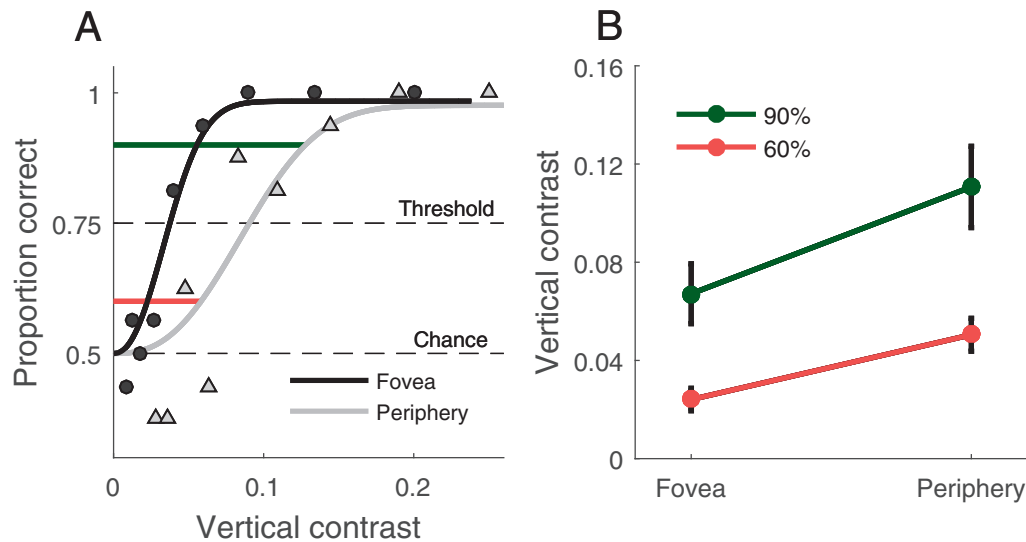


Figure 1. Experiment 1: Fixation task to determine peripheral and foveal contrast thresholds. (A) Psychometric functions for one exemplary observer. The red and the green line correspond to 60% and 90% correct, respectively. (B) Average vertical contrasts for the fovea and the periphery that correspond to 60% (red) and 90% (green) performance. Error bars are 95% confidence intervals.

either cw or ccw by 10° from the vertical axis indicating that participants now have to respond. By two additional buttons on the keyboard, participants could switch between the two possibilities and select the one that they thought matched the vertical plaid orientation (two-alternative forced choice; 2AFC). Participants received one point for a correct answer (+1), and minus one point (−1) for an incorrect answer. This score and their overall score was shown after each trial, separated by a vertical bar (e.g., +1 | 20). Additionally, a sound with a frequency of $f_{\text{low}} = 350$ Hz was played in case of a wrong answer. When participants did not maintain fixation, a sound with a higher frequency of $f_{\text{high}} = 500$ Hz was played. In total, the fixation task comprised 288 trials [9 (contrast values) \times 2 (eccentricities) \times 2 (orientations) \times 8 (repetitions)], which were recorded in one session lasting about 40 min. This experiment was recorded in the same session directly after the saccade-only task.

Individual responses were transformed into proportion-correct choices for every stimulus value, separately for both viewing conditions (fovea, periphery). We then fitted Weibull functions to the data using Psignifit-4.0 software (Schütt, Harmeling, Macke, & Wichmann, 2016) and inverted them to retrieve contrast values, which correspond to 60% (below threshold) or 90% (above threshold) correct performance, respectively.

Figure 1A depicts psychometric functions for one observer; Figure 1B depicts average values for the above (A) and below (B) threshold values. On average, retrieved contrast values were higher in the periphery ($M = 0.081$, $SD = 0.02$) than in the fovea ($M = 0.046$, $SD = 0.015$), and higher for the above- ($M = 0.089$, $SD = 0.025$) than for below-threshold values ($M = 0.037$,

$SD = 0.01$). To test that A and B values differ significantly, we entered the data in a 2×2 ANOVA with the factors eccentricity (fovea, periphery) and discriminability (above, below). Results reveal a main effect of discriminability, $F(1, 15) = 100.28$, $p < 0.001$, indicating that above values are higher than below values. Moreover, the main effect of eccentricity, $F(1, 15) = 72.74$, $p < 0.001$, shows that for identical performance less contrast is required for foveal than for peripheral vision. Due to a difference between the slopes of the foveal and peripheral psychometric functions, contrast differences between foveal and peripheral vision are larger for above- versus below-threshold values. This is reflected in the discriminability \times eccentricity interaction, $F(1, 15) = 6.24$, $p = 0.025$.

Perceptual saccade task

For the perceptual saccade task (Figure 2), participants were instructed to judge the vertical component of the plaid stimulus and that they may move their eyes. The trial initiation was identical to the fixation task. Plaid stimuli only appeared in the periphery and were displayed for 450 ms. The fixation cross remained visible for an additional 200 ms (overlap paradigm). The contrast of the plaid was derived from individual psychometric functions and could either be above (A) or below (B) peripheral threshold. As soon as the eye exceeded a distance of 2° from the fixation cross, the target was swapped to foveal contrast and could either be above (A) or below (B) foveal threshold for the remaining time. Afterward, participants had to respond via a keyboard press. As in the fixation task, participants received +1 point for a correct and −1

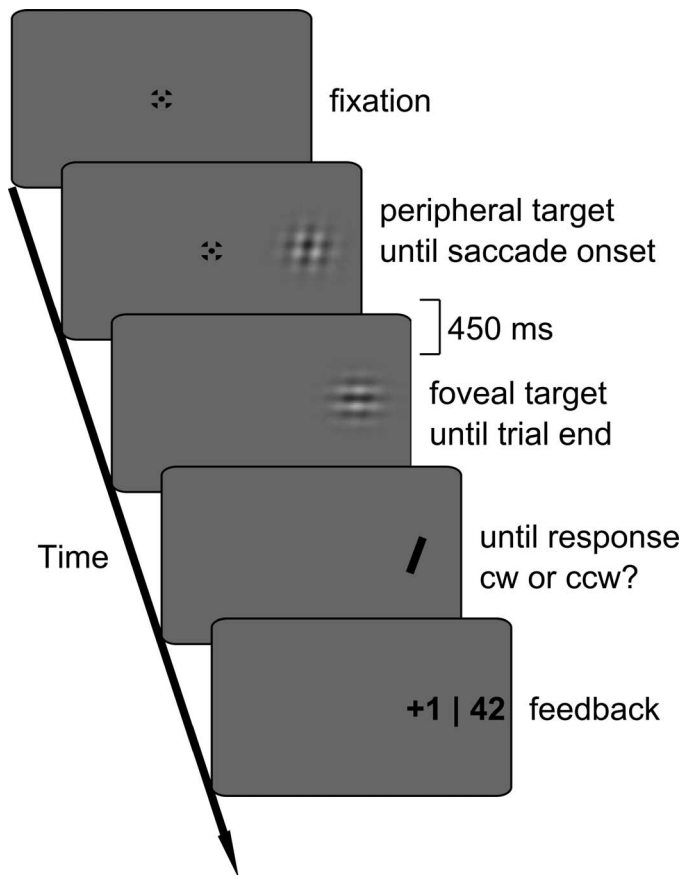


Figure 2. Experiment 1: Trial procedure for the perceptual saccade task. Participants fixated at the screen center and started each trial by pressing a button on a keyboard. After a random time between 750–1500 ms, a plaid appeared in the periphery. The plaid consisted of a horizontal sine wave aligned to the cardinal axis and a vertical sine wave that deviated by 10° either clockwise (cw) or counterclockwise (ccw). Participants were instructed to judge whether the orientation of its vertical component was cw or ccw and they were allowed to move their eyes. The contrast of the vertical relative to the horizontal component was either above or below the individual peripheral threshold. During the saccade, the relative contrast was adjusted to be either above or below the foveal threshold. The fixation cross was extinguished after 200 ms and the plaid was presented for 450 ms. Afterward, participants had to indicate the vertical orientation (cw or ccw) via a keyboard button press and received feedback. Stimuli are not drawn to scale.

point for an incorrect answer. This score and their overall score were shown after each trial, separated by a vertical bar (e.g., +1 | 20).

As peripheral and foveal discriminability could be above or below threshold, independent of each other, we had a 2×2 design with four possible conditions (A–A, A–B, B–A, B–B). The experiment consisted of four blocks with 200 trials each. In each block, we tested two of the conditions against each other. Conditions were arranged such that the target appeared to the left of

fixation for the first condition and to the right of fixation for the second condition. This arrangement was counterbalanced across participants. Specifically, we tested A–A versus B–B, A–A versus B–A, B–A versus B–B, and A–B versus B–A. The whole experiment thus consisted of 800 trials and was recorded in one session, lasting between 1.5 and 2 h. Participants were told that blocks might differ with regard to difficulty, but they were neither informed about the gaze-contingent display nor about the specific conditions tested. After each block, participants often reported that the task at one of the two hemifields was particularly difficult, but they did not report the change of the target during the saccade.

Saccade-only task

Thirteen of our 16 participants had previously participated in the saccade-only task. The trial procedure was identical to that of the perceptual saccade task, except that there was no perceptual task at the end of each trial. After the plaid had disappeared, the fixation cross immediately appeared at the screen center to indicate that participants could start the next trial. Participants were instructed to look as quickly as possible at the appearing plaid. Plaids could either appear in the left or right hemifield and the vertical component could either be tilted cw or ccw. Within a trial, the plaids' contrast did not change and belonged to one of five contrast values (vertical contrast: 0.04, 0.0566, 0.08, 0.1131, and 0.16). In total, participants completed two blocks of 160 trials each, which lasted between 20–30 min and were recorded in the same session as the fixation task.

Eye movement analysis

Saccades were detected using the EyeLink 1000 (SR Research Ltd.) algorithm. Latencies were defined as the first saccadic sample with respect to target onset. To obtain peak velocities, we took the maximum of the differentiated eye position signals. In the perceptual saccade task, we removed trials with latencies below 100 ms and above 400 ms, which applied to 569 trials (4.5%). Latencies below 100 ms are likely to be caused by anticipation and not in response to the target, whereas with a latency above 400 ms, no foveal vision was provided as targets were presented for 450 ms. Removed trials were equally represented across conditions. We additionally discarded 211 further trials because the eye position was more than 2° away from the fixation cross while the target appeared (1.7%). Thus, our latency analysis is based on 12,020 of a total of 12,800 recorded trials (93.9%). For the analysis of peak velocities, we did not consider trials with missing samples during a saccade. This applied to a further 410

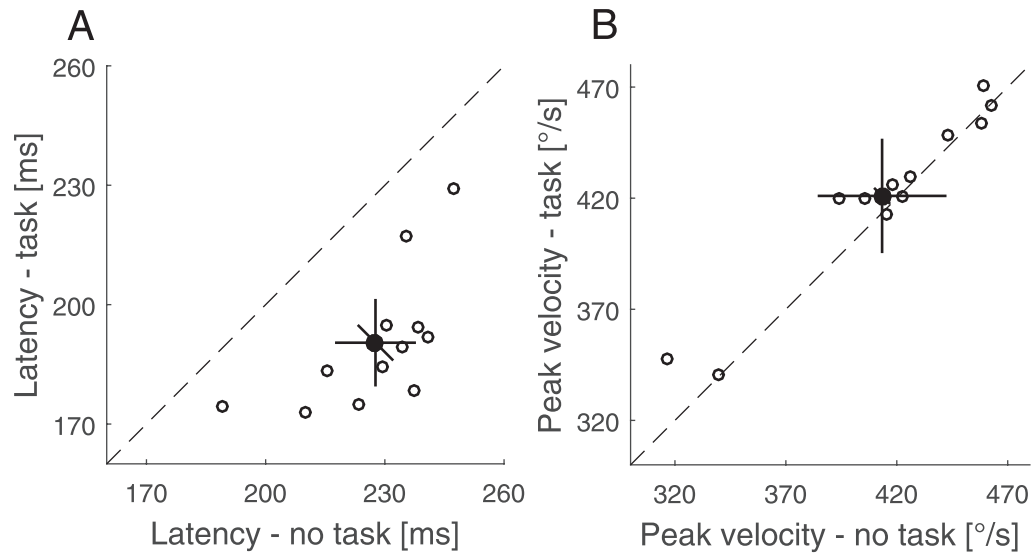


Figure 3. Experiment 1: Effect of a perceptual task. Saccade latency (A) and peak velocity (B) averaged across all four perceptual saccade task conditions (task) against values from the saccade-only task (no task). Black circles are averaged data with 95% confidence intervals. Diagonal error bars mark the error of the differences between the two conditions and have to be compared to the identity line. Open circles denote data from individual observers.

trials. The same criteria applied to the saccade-only task. Here, 336 of 4,160 trials (8.1%) were discarded as their latencies were not in the given time window, and additional 118 trials were not considered for the analysis of peak velocities.

Results

The effect of a perceptual task

In the saccade-only task, the average saccade latency was 226 ms ($SD = 16$ ms) and latencies did not vary as a function of the plaids' contrast ratio. Average latencies for the five different contrast values were 226, 223, 228, 226, and 226 ms when the contrast of the vertical grating was 0.04, 0.057, 0.08, 0.113, and 0.16. A linear regression of the saccade latencies on these contrast values revealed a slope of $b = 4.4$ ms. Thus, according to the regression, changing the contrast from 0.04 to 0.16 would increase the latency by about 0.5 ms. A one-way repeated measures ANOVA also revealed that the contrast ratio of the plaids did not influence saccade latencies ($F < 1$). Average and individual latencies from the perceptual saccade task and the saccade-only task can be found in Figure 3A. With a perceptual task, the average saccade latency decreased by 36 ms to 190 ms, $t(11) = 9.17$, $p < 0.001$ (range: 15–60 ms).

We also found higher peak velocities with ($M = 421$ °/s, $SD = 41$ °/s) compared to without-perceptual task ($M = 413$ °/s, $SD = 45$ °/s), $t(11) = 2.33$, $p = 0.04$ (Figure 3B). According to the saccadic main sequence, peak velocities are known to increase with saccade amplitudes (Bahill, Clark, & Stark, 1975), so we assessed

whether this difference in velocities was caused by a difference in amplitudes. Therefore, we first compared saccade amplitudes in the perceptual saccade ($M = 12.16^\circ$, $SD = 0.15^\circ$) and the saccade-only task ($M = 12.05^\circ$, $SD = 0.23^\circ$). We did not find any statistical evidence for larger amplitudes with a perceptual task at hand, $t(11) = 2.03$, $p = 0.067$. However, an absence of statistical significance is not evidence that amplitudes are actually identical. Furthermore, the amplitude difference was in the same direction as the difference in peak velocity, as expected by the main sequence. Therefore, we also computed a velocity index that was corrected for amplitude. The velocity index, V_I , was defined as the saccade's peak velocity divided by the square root of its amplitude (Lebedev, Van Gelder, & Tsui, 1996). Mean velocity indices, V_I , were 121 ($SD = 11$) with and 119 ($SD = 13$) without perceptual task and did not differ significantly, $t(11) = 1.56$, $p = 0.147$. Moreover, and unlike the study by Bieg et al. (2012), we did not find any evidence for decreasing latency differences and increasing peak velocity differences over the duration of the experiment (Supplementary Figure S1).

The effect of peripheral and foveal discriminability

We entered saccade latencies from the perceptual saccade task (Figure 4A) in a 2×2 ANOVA with the factors foveal and peripheral discriminability, both with the levels above and below. If saccade latencies were modulated by information gain, this would have resulted in a significant interaction. The ANOVA

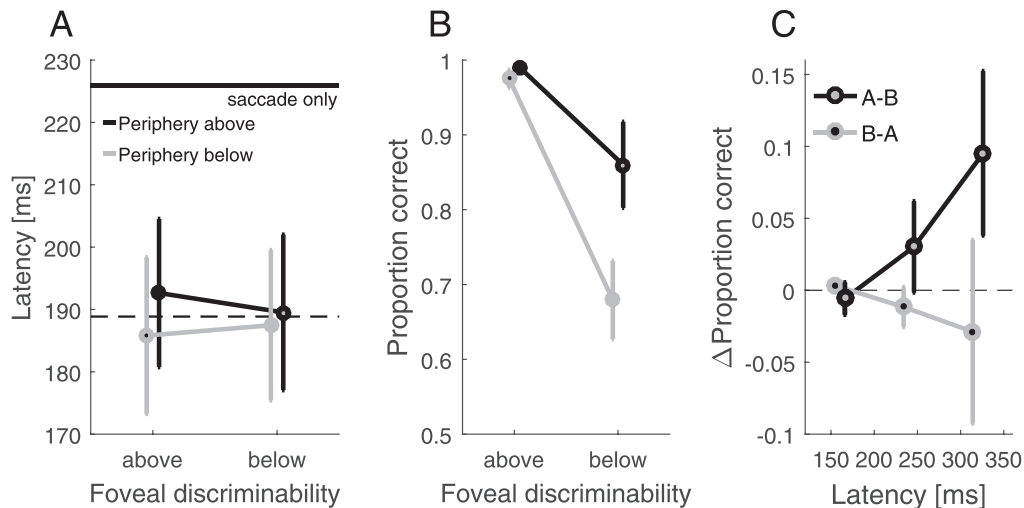


Figure 4. Experiment 1: Effect of peripheral and foveal discriminability. (A) Average saccade latencies in the four different conditions. Error bars are 95% confidence intervals of between-participant variability. The dashed horizontal line represents the average latency in all conditions with a perceptual task, and the solid black line represents the average latency without a perceptual task. (B) Average perceptual performance for the four different conditions, with error bars denoting 95% confidence intervals. (C) Relative performance as a function of latency in the perceptual saccade task for the A–B and B–A condition. Proportion of correct responses subtracted by the individual mean in each condition for three 80 ms bins centered on 160, 240, and 320 ms. Error bars denote 95% confidence intervals of between-participant variability. Values are slightly offset for better visibility.

revealed a main effect of peripheral discriminability, $F(1, 15) = 8.54$, $p = 0.011$. Saccade latencies were lower by about 4 ms when the peripheral discriminability was below ($M = 187$ ms, $SD = 25$ ms) compared to above threshold ($M = 191$ ms, $SD = 24$ ms). We neither observed a main effect of foveal discriminability, $F(1, 15) = 0.16$, $p = 0.698$, nor an interaction, $F(1, 15) = 2.25$, $p = 0.154$. For peak velocities, no differences were observed (all $F < 1$).

One possible explanation for the absence of a noteworthy latency modulation would be that our manipulation of target discriminability did not affect perception in the first place. If our manipulation was successful, then (a) performance should differ across the different conditions, and (b) performance in the B–A and the A–B conditions should depend on the saccade latency. To confirm that our manipulation of target discriminability was indeed successful, we first compared performance across the different contrast conditions (Figure 4B). Performance was best in the A–A condition ($M = 0.99$, $SD = 0.01$), worst in the B–B condition ($M = 0.68$, $SD = 0.10$), and intermediate for the A–B ($M = 0.86$, $SD = 0.11$) and the B–A ($M = 0.98$, $SD = 0.02$) conditions. A nonparametric Friedman test of repeated measures revealed that performance in the conditions differed significantly, $X^2 = 36.84$, $p < 0.001$. In order to test whether performance was better with above-threshold foveal information, we compared performance in the A–A condition with the A–B condition and the B–A condition with the B–B condition using Wilcoxon signed rank tests. Perfor-

mance in the A–A condition was significantly better than in the A–B condition, $Z = -3.35$, $p < 0.001$, and performance in the B–A condition was significantly better than in the B–B condition, $Z = -3.41$, $p < 0.001$. To test effects of peripheral discriminability, we compared performance in the B–A with A–A conditions as well performance in the B–B with the A–B conditions. With below-threshold foveal information, above-threshold peripheral information improved performance, B–B versus A–B: $Z = -3.29$, $p < 0.001$. When foveal information was above threshold, the performance benefit due to peripheral discriminability failed to reach significance, A–A versus B–A, $Z = -2.45$, $p = 0.014$ (Bonferroni-corrected alpha level: $\alpha' = 0.0125$).

The second important prediction from our manipulation was that performance in the A–B condition as well as the B–A condition should depend on the saccade latency: When peripheral information is above threshold and foveal information is below threshold (A–B), performance should increase with higher latencies, because above-threshold peripheral information would be available for a longer duration. It should be the other way round for the B–A condition. To test this prediction, we split the data into three 80 ms bins centered on 160, 240, and 320 ms. For each participant in every bin, we computed the proportion correct relative to the individual mean in the respective condition (Figure 4C). We compared the data using a 3 (latency bins) \times 2 (conditions) repeated-measures ANOVA. The ANOVA revealed a significant latency

bin \times condition interaction, $F(2, 18) = 6.73$, $p = 0.007$, suggesting that performance depended on the saccade latency. To quantify how much participants would have benefitted by adjusting their reaction time, we computed linear regressions on the relative performance values over the three latency bins. Relative performance values were averaged across participants. The regressions revealed a slope of $b_{A-B} = 0.63 \text{ s}^{-1}$ for the A–B and a slope of $b_{B-A} = -0.20 \text{ s}^{-1}$ for the B–A condition. This suggests that by delaying a saccade from the fastest percentile (113 ms) to the slowest percentile (332 ms), participants' performance would have increased by 13.8% in the A–B condition and it would have decreased by 4.4% in the B–A condition.

Discussion

We measured saccade latencies to plaid stimuli, which also served as target for a perceptual task. With a perceptual task, latencies were reduced by 36 ms compared to a saccade task without perceptual judgment. The magnitude of the latency difference between task-related and target-elicited saccades reported here is in line with previous findings (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trotter & Pratt, 2005). Additionally, we independently manipulated peripheral and foveal discriminability of the plaids task-relevant vertical component by changing its contrast during the saccade. Saccade latencies were not modulated by information gain, but they were lower by about 4 ms when peripheral contrast was below threshold. Compared to the 36-ms facilitation by a perceptual task, this effect is negligibly small and we conclude that the differences in information gain do not modulate the facilitating effect of a perceptual task.

We also found higher peak velocities when the saccade was accompanied by a perceptual task. Although there was no statistical difference in amplitudes, this peak velocity effect vanished when corrected for saccade amplitude (Lebedev et al., 1996). Therefore, we cannot dismiss the possibility that the difference in peak velocity is confounded with tiny yet systematic differences in amplitude. One possible analysis to avoid this confound would have been to look at the whole main sequence relationship between amplitude and peak velocity (Bahill et al., 1975). As we were primarily interested in latency effects, we did not vary saccade amplitude and are therefore not able to explore the main sequence relationship.

Bray and Carpenter (2015) recently reported reduced latencies to informative targets. They varied whether a first saccade target (colored dot) reliably indicated the position of the second saccade target or not. They labeled the reliable first target as being an informative target and the unreliable one as being an uninformative

target. In their experiment, latencies are reduced when the target reliably indicates the destination of the forthcoming saccade (Bray & Carpenter, 2015). However, their definition of informativeness differs drastically from ours. Whereas their definition concerns the external reliability of a saccade target, our definition of information gain involves the internal comparison of foveal and peripheral vision and thus, the informativeness of the saccade itself given the constraints of the visual system. In contrast to that, their task (Bray & Carpenter, 2015) does not necessarily involve the comparison of peripheral and foveal vision, but could be solved with peripheral vision alone.

The independent manipulation of peripheral and foveal discriminability in our experiment also changed how much information observers gathered by executing a saccade. The condition in which the plaid was presented below threshold in the periphery but changed to above threshold once foveated (B–A) mimicked normal saccades, in which people gained information by making saccade eye movements. The opposite is true for the A–B condition, in which people actually lost information by executing the saccade. Performance in the B–A condition indeed decreased with increasing latency and it increased with increasing latency in the A–B condition. Because participants were only instructed to solve the task and had 450 ms to discriminate the target, the optimal response in the A–B condition would have been to delay the saccade as much as possible or to not saccade to the target at all. Nevertheless, observers neither omitted the saccade, nor did they delay their eye movement in order to benefit longer from peripheral vision.

In order to compute a saccade's gain in information, the visual system would have to compare the presaccadic peripheral and postsaccadic foveal discriminability. Since foveal information is only available after executing the saccade, the information gain has to be estimated before saccade preparation based on the predicted foveal information. This prediction would then have to be updated over the time course of the experiment. It might be that this learning did not take place, although prior research showed that the oculomotor system is generally able to adjust the distribution of reaction times given the constraints of a task (Jarvstad, Rushton, Warren, & Hahn, 2012; Madelain, Champrenaut, & Chauvin, 2007; Schütz et al., 2012). Moreover, computing the information gain would require a separate representation of information obtained from peripheral and foveal samples of the stimulus. Such a separate representation would not be given when the information from both samples is combined into a single representation of the object and its features. Thus, one possible explanation why latencies did not differ across conditions might be that the oculomotor system does not have separate access to

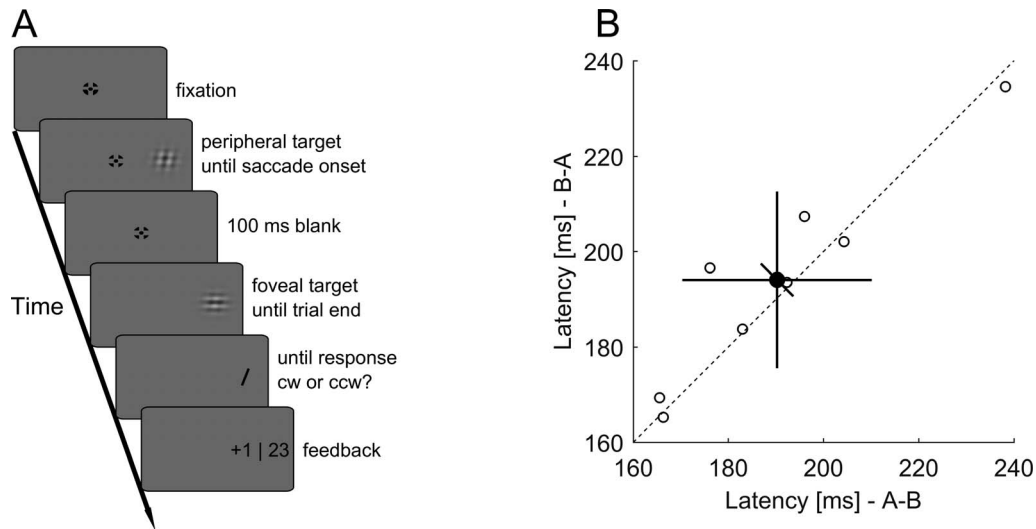


Figure 5. Experiment 2: Effect of peripheral and foveal discriminability with target blanking. (A) The trial procedure for Experiment 2 was identical to the perceptual saccade task in Experiment 1 (Figure 2), with the only exception being the introduction of a 100-ms blank during the saccade. The target (including blank) was presented for 550 ms. (B) Average latency in the B–A versus latency in the A–B condition. Diagonal error bars mark the error of the difference between the two conditions, and have to be compared against the diagonal. Open circles denote individual data.

peripheral and foveal discriminability because both the peripheral and foveal information are integrated into a common trans-saccadic percept (Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015).

Experiment 2: Target blanking

In Experiment 1, we replicated the finding that saccade latencies are reduced whenever people engage in a perceptual discrimination task at the saccade target. Furthermore, the present results show that this facilitation was not modulated by peripheral and foveal discriminability. As mentioned above, one possible explanation might be that participants integrated peripheral and foveal information (Ganmor et al., 2015; Wolf & Schütz, 2015) and therefore lost separate access to peripheral and foveal information. If peripheral and foveal information is not accessible separately, the gain or loss of information by a saccade cannot be computed and as a consequence cannot modulate saccade latencies. Thus, we wanted to guarantee in Experiment 2 that participants do not integrate peripheral and foveal information, but have separate access to peripheral and foveal discriminability. Therefore, we introduced a target blank shortly after the eye landed. Blanking the target is known to make information from pre- and postsaccadic samples separately accessible (Deubel, Schneider, & Bridgeman, 1996; Weiß, Schneider, & Herwig, 2015).

Methods

We recorded data from nine participants who were all undergraduate students from Giessen University. Data from one participant were excluded from the analysis because more than 80% of trials were corrupted with blinks. The remaining eight participants whose data were considered for the analysis had a mean age of 21 years (range: 18–24 years; seven women, one man). The setup was identical to the previous experiment. We measured saccade latencies to peripherally appearing plaids in an above to below (A–B) and a below to above (B–A) threshold condition (Figure 5A). Again, the contrast of both gratings added up to 0.4 and the vertical contrast was set to the average values derived from Experiment 1 (Figure 1B). Specifically, in the A–B condition, the vertical contrast was set to 0.111 for peripheral and 0.024 for foveal vision. In the B–A condition, it was set to 0.05 (periphery) and 0.067 (fovea). The trial procedure was identical to Experiment 1 with the only exception being that the target disappeared for 100 ms (blank) as soon as the eyes exceeded the critical distance of 1.5° from the fixation cross. Afterward, the target was displayed at foveal contrast until the end of the trial (450 ms after target onset). Identical to Experiment 1, participants had to indicate the orientation of the vertical component which was tilted cw or ccw. Data from the A–B and the B–A conditions were obtained in the same session, and for every observer, one condition was assigned to each hemifield. This assignment was balanced across participants. The experiment com-

prised 400 trials and lasted approximately one hour. We discarded trials with an eye movement latency below 100 ms and above 400 ms. In total, 95.4 % of trials were considered for the final analysis.

Results

Figure 5B depicts average saccade latencies in both conditions for every observer. In the A–B condition, the average saccade latency was 190 ms ($SD = 23$ ms), in the B–A condition, it was 194 ms ($SD = 22$ ms). We found no significant difference between latencies in the A–B and the B–A condition, $t(7) = 1.33$, $p = 0.23$. In the A–B condition, performance was 80% correct ($SD = 18\%$), whereas in the B–A condition, participants achieved 97% correct responses ($SD = 2\%$). A Wilcoxon signed rank test revealed that performance differed significantly between the two conditions, $Z = -2.24$, $p = 0.025$.

Discussion

Here we tested whether the manipulation of information gain affects saccade latencies when a blank is included between the peripheral and foveal target. Target blanking is known to make information from peripheral and foveal samples separately accessible (Deubel et al., 1996; Weiß et al., 2015). We tested one condition wherein observers gained information (B–A) against another condition in which they lost information by making a saccade (A–B). As in Experiment 1, we did not find any evidence for information gain influencing saccade preparation. This means that the lack of an effect could not be explained by potentially mandatory integration of peripheral and foveal information (Ganmor et al., 2015; Oostwoud Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015).

Experiment 3: The probability of a perceptual task

Milstein and Dorris (2007) found a linear relationship between saccade latencies to single targets and the expected value associated with those targets. Expected value can be computed as the product of reward magnitude and reward probability. Milstein and Dorris (2007) independently manipulated these two factors to obtain targets with different expected values. Saccade latencies correlated with both reward magnitude and probability, but best with expected value—the combination of the two. In Experiments 1 and 2 we have shown that saccade latencies did not depend on the

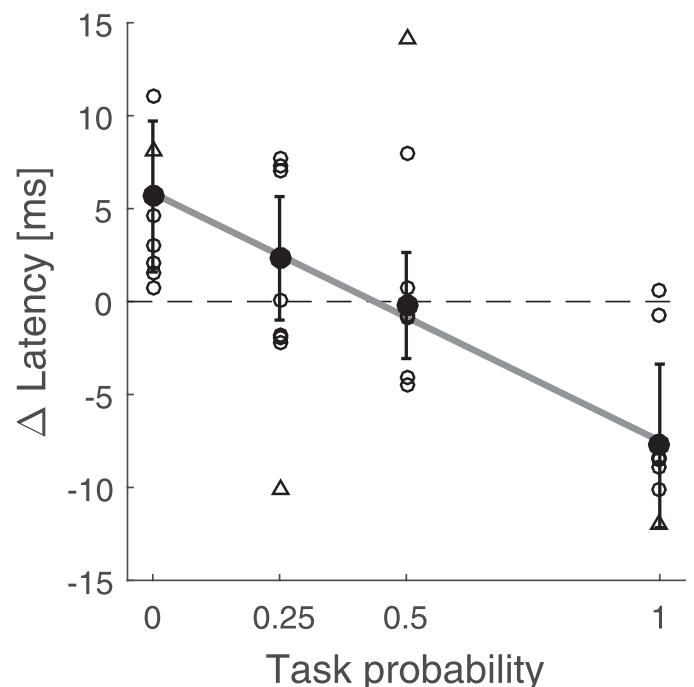


Figure 6. Experiment 3: Effect of task probability. Latency relative to individual mean as a function of task probability with 95% between-participant variability. Open circles denote individual data. Open triangles are data from the participant who was labeled an outlier. The solid gray line is a linear regression through the aggregated data (slope: -13.3 ms).

gain in information (in contrast to reward magnitude). In all our perceptual task conditions, the probability of a perceptual task was always unity. Thus, the informational value was identical to the gain in information. In this experiment, we want to test whether the second factor in Equation 1, task probability, affects saccade preparation and yields a linear relationship with saccade latencies.

Methods

We recorded data from eight observers, the same observers who also completed Experiment 2. Data from one participant was not included in the final analysis because the average latency in two conditions deviated by more than 2 standard deviations (Figure 6, open triangles). Stimuli were again plaid stimuli with a vertical contrast of 0.05. The experiment consisted of four blocks of 200 trials each. Within each block, targets could appear either on the right or on the left side of the screen. Participants were instructed to saccade to the target and, if applicable, report its orientation. They were told that the blocks differ with regard to the probability that they will have to respond. At the end of the trial, either the fixation cross appeared at the screen center to show that they may

continue with the next trial or a bar appeared at the target position to show that they have to report the orientation of the vertical component. Within one block, there was one fixed probability that observers had to respond. Task probabilities were 0, 0.25, 0.5, and 1. Again, we discarded trials with too early (<100 ms) or too late (>400 ms) saccades. This applied to 255 trials (9.1%).

Results

For every observer in every probability condition, we computed the average latency relative to the individual mean across conditions. The average latency differences decreased with increasing task probability from 5.7 ms ($p_{\text{task}} = 0$, $SD = 6$) over 2.3 ms ($p_{\text{task}} = 0.25$, $SD = 5$) and -0.2 ms ($p_{\text{task}} = 0.5$, $SD = 4$) to -7.7 ms ($p_{\text{task}} = 1$, $SD = 6$). Average and individual values are depicted in Figure 6. We compared saccade latencies using a repeated-measures ANOVA with the factor task probability. The ANOVA revealed a significant main effect of task probability, $F(3, 18) = 5.96$, $p = 0.005$. We determined the mean latency for each task-probability condition by averaging across all observers and computed a regression of these mean latencies on task probability. The regression revealed a slope of -13.3 ms and explained 99% of variance.

Discussion

The present experiment tested whether saccade latencies decrease linearly with the probability that information obtained at the saccade target is task-relevant. Participants saccaded to plaid stimuli in the periphery. Across blocks, we varied the probability that observer had to report the orientation of the plaids' vertical component. We found that the probability of a perceptual task affected saccade latencies. Latencies decreased linearly with increasing task probability.

The average latency difference when observer had to respond throughout ($p_{\text{task}} = 1$) and the condition without perceptual task ($p_{\text{task}} = 0$), yielded a value of 13.3 ms. This difference is smaller than in the results of Experiment 1 and the values reported in the literature (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). One possible explanation might be that observers did not represent the task probabilities veridically, but instead biased them towards the mean task probability. This would agree with classic findings on the misrepresentation of extreme probabilities outlined in prospect theory (Kahneman & Tversky, 1979). Thus, observers might have expected a perceptual task even in the zero

probability condition and they might have expected the absence of a perceptual task even in the 100% condition.

Experiment 4: The perceptual task effect is spatially specific

In Experiment 3, we found that the facilitation due to a perceptual task is modulated by task probability. Because task probability within one block was the same for both hemifields, we do not yet know whether this facilitation is spatially selective or caused by global arousal. If the facilitation was not spatially selective, it could explain the absence of a noteworthy latency modulation in Experiment 1. In Experiment 1, we always tested two conditions of different information gains against each other, one assigned to each hemifield. As a consequence, differences might have averaged out. In this experiment, we aim to show that our results are not affected by global arousal but that the perceptual task effect is spatially specific.

Methods

Participants were five undergraduate students from Giessen University (mean age: 26 years; age range: 20–30 years; four women, one man). All of them had previously participated in Experiment 1. The setup was identical to the previous experiments. The plaids contrast was set to the individual peripheral below threshold value from Experiment 1 and not modified during a trial or the experiment. Two observers had to perceptually respond whenever the plaid appeared on the left, and the remaining three observers had to perceptually respond to targets in the right hemifield. The experiment consisted of 200 trials and lasted approximately 30 min. We removed 89 out of 1,000 trials for the final analysis due to too early or too late saccade onsets.

Results

Figure 7 depicts individual latencies in the saccade-only and the perceptual saccade task, both from the present experiment, in which both tasks have been interleaved, as well as from Experiment 1, in which they had been recorded in separate blocks. In the present experiment, the average latency is 183.8 ms ($SD = 10.7$ ms) in the perceptual saccade task and 220.3 ms ($SD = 19.7$ ms) in the saccade-only task. Latencies were thus reduced by 36.5 ms due to the presence of a perceptual task. Latencies for the same individuals from Experi-

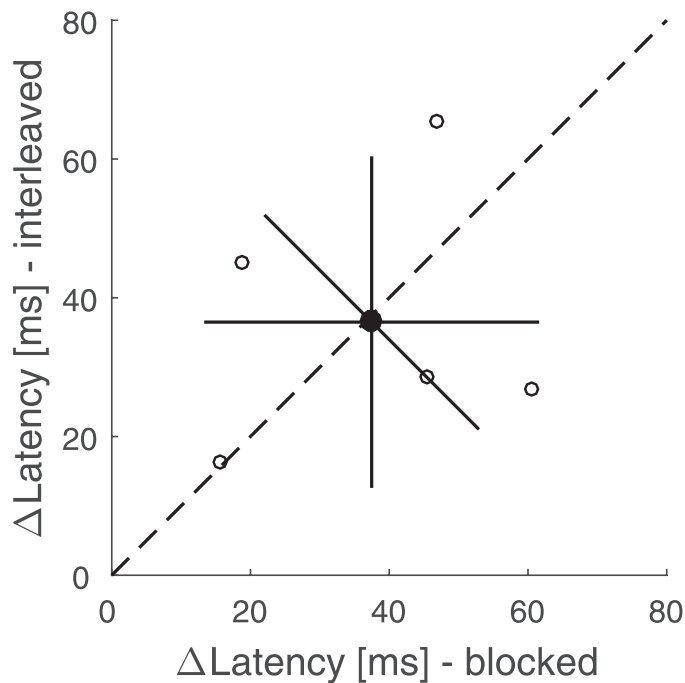


Figure 7. Experiment 4: Spatial specificity of perceptual task. Latency difference between the saccade-only task and perceptual saccade task when both have been recorded in separate blocks against when both have been recorded in the same block. Diagonal error bars mark the error of the difference between the two conditions and have to be compared against the diagonal. Open circles denote individual data.

ment 1 are 199.1 ms ($SD = 23.5$ ms) in the perceptual saccade task and 236.6 ms ($SD = 6.6$ ms) in the saccade-only task. This corresponds to a difference of 37.5 ms. We entered the data into an ANOVA with the two-factors task versus no task and blocked versus interleaved. We obtained a significant main effect of task versus no task, $F(1, 4) = 31.18$, $p = 0.005$. There was neither a significant main effect of blocked versus interleaved, $F(1, 4) = 5.64$, $p = 0.076$, nor a significant interaction, $F < 1$. A Wilcoxon signed rank test revealed that latencies were significantly shorter in the perceptual saccade task, $Z = -2.02$, $p = 0.043$.

Discussion

In this experiment, we have tested whether the effects of a perceptual task are spatially specific. We have compared saccade latencies to one hemifield where participants had to do a perceptual task against latencies to the other hemifield without perceptual task. If the perceptual task effect was caused by arousal, then the latencies to both sides should be similar. We again found shorter saccade latencies to targets that also served as targets for a perceptual task. The latency difference was 36.5 ms and thus in the same magnitude

as in Experiment 1 and previous studies (Bieg et al., 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005). We hereby have replicated the finding that the perceptual task effect is spatially selective and not caused by arousal (Montagnini & Chelazzi, 2005).

Experiment 5: Auditory perceptual task

So far, we have shown that the perceptual task effect is modulated by the probability of a perceptual task and that the facilitation is spatially specific. Thus, it might be caused either by the requirement to foveate task-relevant information and process it with high acuity, or by a general motivation to solve perceptual tasks. In the latter case, shorter latencies should also be observed when the perceptual task is in any modality other than the visual one.

In this experiment, we tested whether saccade latencies are also affected by the presence of an auditory task. Participants saccaded to plaid stimuli and either had to discriminate tones (saccade and auditory task) or ignore them (saccade-only task). Half of the participants had to discriminate a tone that was played as long as the saccade target (continuous tone), the other half had to discriminate a tone that was played as soon as they foveated the saccade target (foveated tone). Continuous tones are equivalent to visual stimuli with regard to their presentation time, whereas foveated tones mimic the foveation behavior of saccades.

Methods

Participants were eight undergraduate students from Marburg University aged between 20 and 26 years (mean age = 23 years; $SD = 2$; six women, two men). None of them had taken part in any of the previous experiments. We recorded eye movements of the right eye using a desktop mounted EyeLink 1000 (SR Research Ltd.) with a sampling rate of 1000 Hz, and the EyeLink Toolbox (Cornelissen et al., 2002). Participant responses were recorded via a standard keyboard. Tones were played via Sennheiser HD 280 Pro headphones (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany).

Participants had to saccade to plaid stimuli either left or right from fixation (Figure 8A). The contrast of the vertical and horizontal components again summed up to 0.4, with the contrast of the vertical component set to 0.2. The horizontal component was aligned to the cardinal axis whereas the vertical component was tilted cw or ccw by 10° . The plaid was continuously displayed

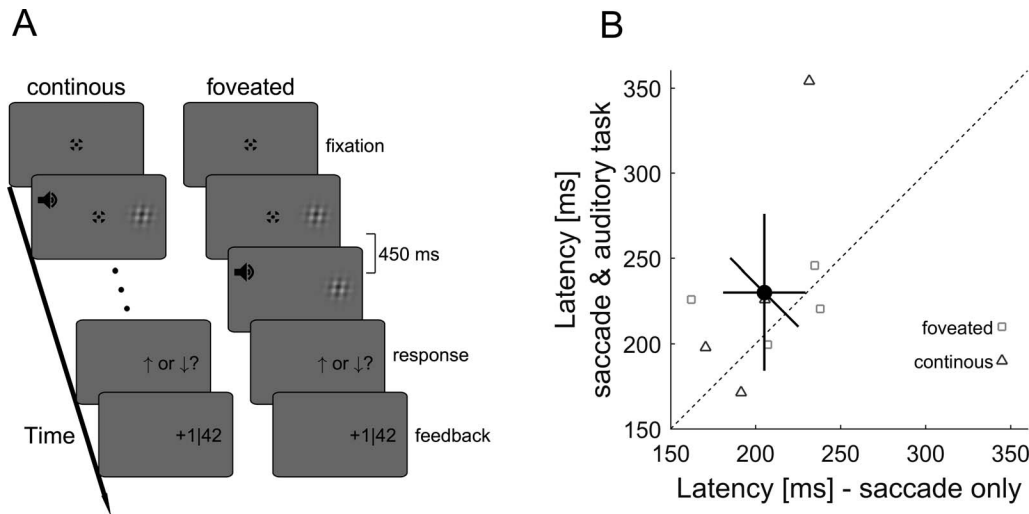


Figure 8. Experiment 5: Effect of auditory perceptual task. (A) Trial procedure for the two auditory perceptual tasks. In the continuous condition, tones were displayed for 450 ms along with the plaid, whereas in the foveated condition, tones were displayed for 100 ms upon foveation of the saccade target. (B) Average and individual latencies in the saccade and auditory task compared to the saccade-only task.

for 450 ms. For half of the participants, a tone was played for 100 ms when they had foveated the plaid (foveated tone; approx. 60 ms after saccade onset) and for the remaining half, it was played as long as the plaid was presented on the screen (continuous tone). Tones were pure tones varying in 8 steps around 440 Hz (396, 418, 429, 434.5, 451, 462, 484, 528) for foveated tones and around 220 Hz (198, 214, 214.5, 217.25, 225.5, 231, 242, 264) for continuous tones. The experiment consisted of two blocks of 200 trials each: One block in which participants were instructed to saccade to the plaid and ignore the tone (saccade-only task) and another block in which participants had to discriminate whether the tone belonged to the higher or to the lower frequencies (saccade and auditory task). For foveated tones, participants were instructed to discriminate the target and were told that the tone was played as soon as the plaid was foveated. For continuous tones, observers were instructed to foveate the plaid and discriminate the tone. The order of conditions was balanced across participants. Every observer completed a practice session of eight trials, which were not included in the analyses. Eye movement analyses were identical to Experiment 1. We discarded 349 out of 3,200 trials due to too short (<100 ms) or too long (>400 ms) latencies. This corresponds to 10.9 % of trials.

On average, observers correctly identified the tones in 86.9 % of trials ($SD = 4.6\%$, range: 80.7%–93.4%). Performance for foveated tones ($M = 86\%$, $SD = 4.7\%$) and continuous tones were in a similar range ($M = 87.8\%$, $SD = 5.1\%$). We converted individual responses into “proportion higher” for each frequency and fitted a cumulative Gaussian to the data using Psignifit-4 (Schütt et al., 2016). Weber fractions (i.e., standard

deviation of the Gaussian divided by the central frequency) were $M = 6.3\%$ ($SD = 1.9\%$). This value is in the range of Weber fractions for pitch discrimination among young healthy individuals (Moore & Peters, 1992).

Results

Saccade latencies for the saccade-only and the saccade and auditory task are depicted in Figure 8B. They were $M = 205$ ms ($SD = 29$ ms; range: 162–238 ms) in the saccade-only task and $M = 230$ ms ($SD = 55$; range: 171–354 ms) in the saccade and auditory task, $t(7) = 1.47$, $p = 0.185$. To test the hypothesis that saccadic reaction time benefits are only present for visual but not for auditory perceptual tasks, we analyzed the present results together with the perceptual (i.e., visual) saccade task and the saccade-only task from Experiment 1. We entered individual mean latencies for the visual and auditory task and the saccade-only tasks in a 2×2 ANOVA. The ANOVA comprised the between-participants factor modality (visual vs. auditory) and the within-participant factor perceptual task (absent vs. present). If there is no benefit for auditory tasks, then we should observe a modality \times perceptual task interaction. The ANOVA revealed a significant interaction, $F(1, 18) = 18.25$, $p < 0.001$. No other effects were observed in the ANOVA (all $F < 1$). The interaction remained significant ($p < 0.001$), even when one participant with extremely high latencies in the auditory task condition was excluded from the analysis (top data point in Figure 8).

Discussion

Here we asked whether the perceptual task effect is restricted to the foveation of visual information or whether it is caused by the motivation to solve a task and therefore also appears with a task in any other than the visual modality. Contrary to the visual modality (Experiment 1), we found no evidence for shorter latencies when participants had to discriminate tones that were either played simultaneously with the saccade target or upon foveation of the saccade target. We conclude that the perceptual task effect is a pure visual phenomenon and thus that shorter saccade latencies are only observed when task-relevant information has to be processed with the fovea.

General discussion

The present study was designed to investigate whether informational value modulates the preparation of saccades similarly as expected motivational value does and whether this can explain the shorter saccade latencies that go along with a perceptual task. We found shorter saccade latencies with than without perceptual task, but this perceptual task effect was not modulated by the information saccades provide in terms of discriminability (Experiments 1 and 2). Saccade latencies decreased with increasing probability of a perceptual task at the saccade target (Experiment 3), and the perceptual task effect vanished when the perceptual task was not in the visual modality but in the auditory modality (Experiment 5). Taken together, our findings suggest that informational value is not used for the preparation of saccade eye movements in an extent comparable to motivational value (Milstein & Dorris, 2007).

The influence of perceptual value on eye movements

A currently discussed question in eye movement research is whether eye movements support perception optimally; that is, whether they maximize the gain in information and thus minimize perceptual uncertainty. One crucial requirement for optimal eye movement control would be a representation of visual uncertainty across the visual field. The fact that people are able to choose the less uncertain stimulus for perceptual judgments (Barthelmé & Mamassian, 2009, 2010) and that peripheral and foveal target information contribute to transsaccadic perception in inverse proportion to their uncertainty (Ganmor et al., 2015; Wolf & Schütz, 2015) suggests that humans do represent perceptual

uncertainty and that this information can be used for perception. Although information about uncertainty seems to be available in the perceptual system, it does not seem to be used consistently to optimize eye movement control. Some studies found that eye movements maximize information gain (Hoppe & Rothkopf, 2016; Najemnik & Geisler, 2005; Peterson & Eckstein, 2012, 2013), while other studies found clearly suboptimal eye movement behavior (Morvan & Maloney, 2012; Verghese, 2012) or mixed results (Eckstein, Schoonveld, Zhang, Mack, & Akbas, 2015; Renninger et al., 2007; Schütz et al., 2012). Another study (Ackermann & Landy, 2013) showed that the endpoints of initial saccades are clearly biased by the expected value to correctly locate a target in a rewarded target region, but endpoints are not optimal with regard to the gain in information. These widely different results suggest that the optimality of eye movements might depend very much on the task and the stimuli.

In the current study, we did not find any evidence that this information is used to modulate and optimize the preparation of saccades. If eye movements supported perception optimally, we should have observed shorter latencies when people can gain information by making an eye movement and longer latencies when people cannot gain or actually can lose information. Instead, latencies tended to be similar across all conditions of information gain. Theoretically, all relevant information was available in our paradigm and could have been used for eye movement control. In fact, we showed previously in a very similar paradigm, that the visual system has access to peripheral and foveal uncertainty (Wolf & Schütz, 2015). However, this information did not modulate saccade latencies, not even with a target blank that makes peripheral and foveal information even more accessible. Moreover, the fact that participants continued to execute saccades in the A–B condition when doing so deteriorated their perceptual performance suggests that foveation of task-relevant information is an overlearned and rigid behavior. This behavior might be reinforced by the regular experience of gaining information with foveal vision (Paeye, Schütz, & Gegenfurtner, 2016). Although previous studies showed that learning can shape reaction time distributions (Madelain et al., 2007); that participants are sensitive to the difficulty of a task and can adjust their reaction times accordingly (Jarvstad et al., 2012); or that they can adjust their latencies to increase reward (Schütz et al., 2012), there seems to be a strong urge to directly foveate a target even if this is clearly suboptimal for completing the task at hand (Morvan & Maloney, 2012).

Overlearned and rigid foveation behavior is also reflected in findings with simulated visual field loss. When a central scotoma is simulated, objects can no further be identified with foveal vision. Consequently,

visual search performance is deteriorated drastically (Cornelissen, Bruin, & Kooijman, 2005; Nuthmann, 2014), and compensating for the scotoma requires long-lasting training (Sommerhalder et al., 2004). An exception from this rigid foveation seems to be visual search under scotopic conditions, as eye movement behavior is partially adjusted to the functional scotoma in the fovea during scotopic vision (Paulun, Schütz, Michel, Geisler, & Gegenfurtner, 2015).

The fact that we tested reactive saccades in response to unpredictable, sudden onsets in the periphery might have contributed to the rigid and suboptimal behavior. Typically, saccades with short latencies are less efficient than saccades with longer latencies (Ghahghaei & Vergheze, 2015; Markowitz, Wong, Gray, & Pesaran, 2011; Schütz et al., 2012). In that sense, the general facilitation by the perceptual task might be even counterproductive in our paradigm and prevent an appropriate control of saccades by informational value.

The facilitation by a perceptual task

We replicated earlier studies showing that saccades to targets that also serve as targets for a perceptual task have shorter latencies (Bieg et al., 2012; Guyader et al., 2010; Montagnini & Chelazzi, 2005; Trotter & Pratt, 2005). In addition, we have narrowed down the nature of this facilitation. We found no evidence that it is either influenced by information gain (Experiments 1 and 2) or by differential effects of fatigue or practice, with or without perceptual task. It is also not caused by global arousal, because it is spatially specific (Experiment 4; Montagnini & Chelazzi, 2005). As our stimuli were displayed long enough, we can also rule out explanations based purely on urgency (Montagnini & Chelazzi, 2005). This latter view would be consistent with the absence of a peak velocity difference.

The effect of higher peak velocities with a perceptual task at hand vanished when corrected for subtle differences in amplitude (Experiment 1). Compared to our and other findings (Bieg et al., 2012), the study by Montagnini and Chelazzi (2005) reported a strong increase in peak velocities by about 35°/s compared to without a discrimination task. However, their conditions did not only differ by the presence of the discrimination task but also by urgency, caused by the early and short presentation of the discrimination target. These divergent findings might point to the fact that saccade latency and peak velocity can be manipulated independently with peak velocity being more sensitive to changes in urgency. An alternative explanation would be that the oculomotor system adjusts latency and peak velocity sequentially to achieve an earlier foveation. In a first step, the oculomotor system might reduce response thresholds in

order to achieve shorter latencies (Reddi & Carpenter, 2000) and only then in a second step adjust the motor command to achieve a higher velocity, and thus shorter saccade duration. This strategy would be adaptive, because changes in latency can be comparatively large compared to changes in saccade duration and because stronger motor commands go along with more motor noise and thus higher endpoint variability of the saccade (Harris & Wolpert, 1998).

Another likely cause for the facilitation of a perceptual task might be the general motivation to solve it. The absence of a modulation by information gain (Experiments 1 and 2) and the presence of a modulation by task probability (Experiment 3) might suggest that the facilitation by a perceptual task is primarily caused by such a motivational mechanism. Several studies showed that saccade latencies are sensitive to motivation using reward as a proxy for motivation (Milstein & Dorris, 2007; Takikawa et al., 2002). Motivation can also be manipulated by other means, for example, peak velocities are higher when the saccade target signals the upcoming presentation of a face (Xu-Wilson, Zee, & Shadmehr, 2009). In our task, discrepancies in motivation might have resulted from the visual feedback at the end of each trial. However, differences between task-related and mere target-elicited saccades remain even when controlled for feedback (Bieg et al., 2012). Moreover, when the motivation to solve a task was the only driving cause for this facilitation, then it should also be observed when the discrimination task is in any than the visual modality. However, this is not the case. In our last experiment (Experiment 5), we found no differences in saccade latencies when people had to discriminate auditory rather than visual information. This argues against sheer motivation as the only driving cause of this facilitation.

From our series of experiments, we conclude that the nature of this facilitation is not the motivation to solve a task per se, but the motivation to foveate task-relevant visual information for further processing. Due to the lifelong and overlearned experience that the fovea is the best retinal locus to solve a discrimination task, this earlier foveation seems to occur irrespective of whether it is useful or not.

Keywords: saccade, information gain, value, task-relevance, perceptual task, peripheral vision, foveal vision, latency, reaction time, motivation

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References

- Ackermann, J. F., & Landy, M. S. (2013). Choice of saccade endpoint under risk. *Journal of Vision*, *13*(3):27, 1–20, doi:10.1167/13.3.27. [PubMed] [Article]
- Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences*, *24*, 191–204.
- Barthelmé, S., & Mamassian, P. (2009). Evaluation of objective uncertainty in the visual system. *PLoS Computational Biology*, *5*(9), 1–8.
- Barthelmé, S., & Mamassian, P. (2010). Flexible mechanisms underlie the evaluation of visual confidence. *Proceedings of the National Academy of Sciences, USA*, *107*(48), 20834–20839.
- Bieg, H. J., Bresciani, J. P., Bülthoff, H. H., & Chuang, L. L. (2012). Looking for discriminating is different from looking for looking's sake. *PLoS ONE*, *7*(9), e45445.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Bray, T. J. P., & Carpenter, R. H. S. (2015). Saccadic foraging: Reduced reaction time to informative targets. *European Journal of Neuroscience*, *41*(7), 908–913.
- Chen, L. L., Hung, L. Y., Quinet, J., & Kosek, K. (2013). Cognitive regulation of saccadic velocity by reward prospect. *European Journal of Neuroscience*, *38*(3), 2434–2444.
- Cornelissen, F. W., Bruin, K. J., & Kooijman, A. C. (2005). The influence of artificial scotomas on eye movements during visual search. *Optometry and Vision Science: Official Publication of the American Academy of Optometry*, *82*(1), 27–35.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The EyeLink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*(7), 985–996.
- Eckstein, M. P., Schoonveld, W., Zhang, S., Mack, S. C., & Akbas, E. (2015). Optimal and human eye movements to clustered low value cues to increase decision rewards during search. *Vision Research*, *113*, 137–154.
- Fredericksen, R. E., Bex, P. J., & Verstraten, F. A. (1997). How big is a Gabor patch, and why should we care? *Journal of the Optical Society of America A. Optics, Image Science, and Vision*, *14*(1), 1–12.
- Ganmor, E., Landy, M. S., & Simoncelli, E. P. (2015). Near-optimal integration of orientation information across saccades. *Journal of Vision*, *15*(16):8, 1–12, doi:10.1167/15.16.8. [PubMed] [Article]
- Ghahghaei, S., & Verghese, P. (2015). Efficient saccade planning requires time and clear choices. *Vision Research*, *113*, 125–136.
- Gottlieb, J., Hayhoe, M., Hikosaka, O., & Rangel, A. (2014). Attention, reward, and information seeking. *Journal of Neuroscience*, *34*(46), 15497–15504.
- Guyader, N., Malsert, J., & Marendaz, C. (2010). Having to identify a target reduces latencies in prosaccades but not in antisaccades. *Psychological Research*, *74*(1), 12–20.
- Harris, C. M., & Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, *394*(6695), 780–784.
- Hoppe, D., & Rothkopf, C. A. (2016). Learning rational temporal eye movement strategies. *Proceedings of the National Academy of Sciences, USA*, *113*(29), 8332–8337.
- Jarvstad, A., Rushton, S. K., Warren, P. A., & Hahn, U. (2012). Knowing when to move on: Cognitive and perceptual decisions in time. *Psychological Science*, *23*(6), 589–597.
- Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, *47*(2), 263–292.
- Lebedev, S., Van Gelder, P., & Tsui, W. H. (1996). Square-root relations between main saccadic parameters. *Investigative Ophthalmology and Visual Science*, *37*(13), 2750–2758. [PubMed] [Article]
- Madelain, L., Champrenaut, L., & Chauvin, A. (2007). Control of sensorimotor variability by consequences. *Journal of Neurophysiology*, *98*(4), 2255–2265.
- Manohar, S. G., Chong, T. T., Apps, M. A. J., Jarman,

- P. R., Bhatia, K. P., Husain, M., ... Stamelou, M. (2015). Reward pays the cost of noise reduction in motor and cognitive control. *Current Biology*, 25(13), 1707–1716.
- Markowitz, D. A., Wong, Y. T., Gray, C. M., & Pesaran, B. (2011). Optimizing the decoding of movement goals from local field potentials in macaque cortex. *Journal of Neuroscience*, 31(50), 18412–18422.
- Milstein, D. M., & Dorris, M. C. (2007). The influence of expected value on saccadic preparation. *Journal of Neuroscience*, 27(18), 4810–4818.
- Milstein, D. M., & Dorris, M. C. (2011). The relationship between saccadic choice and reaction times with manipulations of target value. *Frontiers in Neuroscience*, 5, 1–12.
- Montagnini, A., & Chelazzi, L. (2005). The urgency to look: Prompt saccades to the benefit of perception. *Vision Research*, 45(27), 3391–3401.
- Moore, B. C., & Peters, R. W. (1992). Pitch discrimination and phase sensitivity in young and elderly subjects and its relationship to frequency selectivity. *The Journal of the Acoustical Society of America*, 91(5), 2881–2893.
- Morvan, C., & Maloney, L. T. (2012). Human visual search does not maximize the post-saccadic probability of identifying targets. *PLoS Computational Biology*, 8(2), e1002342.
- Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature*, 434(7031), 387–391.
- Nuthmann, A. (2014). How do the regions of the visual field contribute to object search in real-world scenes? Evidence from eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, 40(1), 342–360.
- Oostwoud Wijdenes, L., Marshall, L., & Bays, P. M. (2015). Evidence for optimal integration of visual feature representations across saccades. *Journal of Neuroscience*, 35(28), 10146–10153.
- Paeye, C., Schütz, A. C., & Gegenfurtner, K. R. (2016). Visual reinforcement shapes eye movements in visual search. *Journal of Vision*, 16(10):15, 1–15, doi:10.1167/16.10.15. [PubMed] [Article]
- Paulun, V. C., Schütz, A. C., Michel, M. M., Geisler, W. S., & Gegenfurtner, K. R. (2015). Visual search under scotopic lighting conditions. *Vision Research*, 113, 155–168.
- Peterson, M. F., & Eckstein, M. P. (2012). Looking just below the eyes is optimal across face recognition tasks. *Proceedings of the National Academy of Sciences, USA*, 109(48), e3314–e3323.
- Peterson, M. F., & Eckstein, M. P. (2013). Individual differences in eye movements during face identification reflect observer-specific optimal points of fixation. *Psychological Science*, 24, 1216–1225.
- Reddi, B. A. J., & Carpenter, R. H. S. (2000). The influence of urgency on decision time. *Nature Neuroscience*, 3(8), 827–830.
- Renninger, L. W., Verghese, P., & Coughlan, J. (2007). Where to look next? Eye movements reduce local uncertainty. *Journal of Vision*, 7(3):6, 1–17, doi:10.1167/7.3.6. [PubMed] [Article]
- Schütt, H. H., Harmeling, S., Macke, J. H., & Wichmann, F. A. (2016). Painfree and accurate Bayesian estimation of psychometric functions for (potentially) overdispersed data. *Vision Research*, 122, 105–123.
- Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. *Journal of Vision*, 11(5):9, 1–30, doi:10.1167/11.5.9. [PubMed] [Article]
- Schütz, A. C., Lossin, F., & Gegenfurtner, K. R. (2015). Dynamic integration of information about salience and value for smooth pursuit eye movements. *Vision Research*, 113, 169–178.
- Schütz, A. C., Trommershäuser, J., & Gegenfurtner, K. R. (2012). Dynamic integration of information about salience and value for saccadic eye movements. *Proceedings of the National Academy of Sciences, USA*, 109(19), 7547–7552.
- Sommerhalder, J., Rappaz, B., De Haller, R., Fornos, A. P., Safran, A. B., & Pelizzone, M. (2004). Simulation of artificial vision: II. Eccentric reading of full-page text and the learning of this task. *Vision Research*, 44(14), 1693–1706.
- Takikawa, Y., Kawagoe, R., Itoh, H., Nakahara, H., & Hikosaka, O. (2002). Modulation of saccadic eye movements by predicted reward outcome. *Experimental Brain Research*, 142(2), 284–291.
- Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision: Reinterpreting salience. *Journal of Vision*, 11(5):5, 1–23, doi:10.1167/11.5.5. [PubMed] [Article]
- Thaler, L., Schütz, A. C., Goodale, M. A., & Gegenfurtner, K. R. (2013). What is the best fixation target? The effect of target shape on stability of fixational eye movements. *Vision Research*, 76, 31–42.
- Trottier, L., & Pratt, J. (2005). Visual processing of targets can reduce saccadic latencies. *Vision Research*, 45(11), 1349–1354.
- Verghese, P. (2012). Active search for multiple targets is inefficient. *Vision Research*, 74, 61–71.

- Weiß, K., Schneider, W. X., & Herwig, A. (2015). A “blinking effect” for surface features: Transsaccadic spatial-frequency discrimination is improved by postsaccadic blanking. *Attention, Perception, & Psychophysics*, 77(5), 1500–1506.
- Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, 15(16):1, 1–18, doi:10.1167/15.16.1. [PubMed] [Article]
- Xu-Wilson, M., Zee, D. S., & Shadmehr, R. (2009). The intrinsic value of visual information affects saccade velocities. *Experimental Brain Research*, 196(4), 475–481.