

# Influence of adaptation state and stimulus luminance on peri-saccadic localization

**Katharina Georg**

General Psychology, Department of Psychology II,  
Westfälische Wilhelms-University,  
Münster, Germany



**Fred H. Hamker**

General Psychology, Department of Psychology II,  
Westfälische Wilhelms-University,  
Münster, Germany



**Markus Lappe**

General Psychology, Department of Psychology II,  
Westfälische Wilhelms-University,  
Münster, Germany



Spatial localization of flashed stimuli across saccades shows transient distortions of perceived position: Stimuli appear shifted in saccade direction and compressed towards the saccade target. The strength and spatial pattern of this mislocalization is influenced by contrast, duration, and spatial and temporal arrangement of stimuli and background. Because mislocalization of stimuli on a background depends on contrast, we asked whether mislocalization of stimuli in darkness depends on luminance. Since dark adaptation changes luminance thresholds, we compared mislocalization in dark-adapted and light-adapted states. Peri-saccadic mislocalization was measured with near-threshold stimuli and above-threshold stimuli in dark-adapted and light-adapted subjects. In both adaptation states, near-threshold stimuli gave much larger mislocalization than above-threshold stimuli. Furthermore, when the stimulus was presented near-threshold, the perceived positions of the stimuli clustered closer together. Stimulus luminance that produced strong mislocalization in the light-adapted state produced very little mislocalization in the dark-adapted state because it was now well above threshold. We conclude that the strength of peri-saccadic mislocalization depends on the strength of the stimulus: Stimuli with near-threshold luminance, and hence low visibility, are more mislocalized than clearly visible stimuli with high luminance.

Keywords: saccade, localization, luminance, dark adaptation

Citation: Georg, K., Hamker, F. H., & Lappe, M. (2008). Influence of adaptation state and stimulus luminance on peri-saccadic localization. *Journal of Vision*, 8(1):15, 1–11, <http://journalofvision.org/8/1/15/>, doi:10.1167/8.1.15.

## Introduction

The apparent positions of visual stimuli flashed in the wake of a saccade are distorted (Matin & Pearce, 1965). The distortion is composed of a shift of position along the saccade direction (Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Schlag & Schlag-Rey, 1995) and, in some conditions, a compression towards the saccade target (Bischof & Kramer, 1968; Kaiser & Lappe, 2004; Lappe et al., 2000; Morrone et al., 1997; Ross, Morrone, & Burr, 1997). The shift along saccade direction is spatially uniform across the visual field. Flashes presented between 100 ms before and 30 ms after saccade onset appear shifted in the direction of the saccade. Flashes presented between 30 ms after saccade onset until saccade end appear shifted against the direction of the saccade. The shift has been found under a variety of conditions (Dassonville, Schlag, &

Schlag-Rey, 1995; Lappe et al., 2000; Michels & Lappe, 2004; Morrone et al., 1997) but is most prominently observed under conditions of total darkness (Honda, 1989, 1991; Dassonville, Schlag, & Schlag-Rey, 1992; Lappe et al., 2000; Schlag & Schlag-Rey, 1995). The shift of apparent position in total darkness is believed to arise from an interaction between the retinal position of the stimulus and an extraretinal signal of eye position (Honda, 1991; Pola, 2004). In the presence of a visual background, or visual spatial reference information, the pattern of peri-saccadic mislocalization changes (Bischof & Kramer, 1968; Honda, 1993). It is then dominated by a compression of apparent positions of the flashed objects towards the saccade target (Lappe et al., 2000; Ross et al., 1997). Awater and Lappe (2006) have argued that the compression of flashes towards the saccade target occurs when the positional information of the saccade target is highly reliable and the positional information of the flash is distorted. This happens, for instance, when the target

position is identified by visual reference information and the flash is very brief and of low contrast with regard to the background.

The strength of saccadic compression depends on the contrast of the flashed stimulus (Michels & Lappe, 2004). Low contrast stimuli are more compressed than high contrast stimuli. Presumably, high contrast stimuli are less compressed because they are more salient, allow better identification of their position, and hence provide higher reliability of the position information for the post-saccadic scene reconstruction process. Thus, the variation of the intensity of the flash may be a tool to vary the amount of compression. We therefore asked whether compression may become apparent in total darkness if the intensity of the flash is reduced.

The state of dark adaptation of the subject is an important parameter in experiments on localization of flashed objects in the dark. In the dark-adapted state, flashes of a particular luminance and duration appear brighter and longer lasting than in the light-adapted state. Dark adaptation lowers the luminance detection threshold. Dark adaptation may also influence the pattern of mislocalization. In the experiments described in the following, we therefore measured peri-saccadic mislocalization in dark-adapted and light-adapted conditions and with near-threshold and above-threshold stimuli.

## General methods

### Subjects

Five subjects (2 female, 3 male, 26 to 31 years, all with normal or corrected vision) participated in the experiments. All participants were experienced in psychophysical studies but naive to the objective of the current research, except KA, who is one of the authors.

### Visual stimuli and general setup

Experiments were conducted in a completely dark room with luminance below  $0.0006 \text{ cd/m}^2$ . The head of the subjects was supported by a chin rest during the experimental session. Stimuli were presented on a 19-in. monitor (Samsung 95P plus) with a visible display size of  $37 \text{ cm} \times 27.5 \text{ cm}$ . The viewing distance of  $40.5 \text{ cm}$  to the screen resulted in a visual field of  $49^\circ \times 28.5^\circ$ . The display had a resolution of  $800 \times 600$  pixels and a frame rate of 120 Hz. A transparent dark gray foil was attached to the screen to further reduce the luminance by about 2 log units. This was done to allow the presentation of very dim stimuli and to eliminate the view of the edges of the display area. The foil fully eliminated the view of the

edges of the display area in both the dark-adapted and light-adapted conditions.

Eye movement data were recorded by a video-based eye tracker (EyeLink II, SR Research). The eye position was tracked by an infrared camera and was measured with a sample rate of 250 Hz.

The stimulus was a vertical bar ( $0.5^\circ \times 28.5^\circ$ ) that appeared at one out of four possible positions distributed equidistantly around the saccadic target. The luminance of the stimulus could be either near or well above threshold. Prior to the experiment, we determined the detection thresholds for flashed stimuli in dark-adapted and light-adapted states for each subject (see Figure 2). Fixation point ( $0.5^\circ \times 0.5^\circ$ ) and saccadic target ( $0.5^\circ \times 0.5^\circ$ ) had a luminance of  $0.046 \text{ cd/m}^2$ .

Frame presentation times of the display at 120 Hz were 8 ms. To verify that the phosphor persistence of the stimuli on the monitor was shorter than the values of the frame rate, we measured with a photocell the temporal luminance profile on the monitor for the three stimuli (Figure 1). All curves dropped to baseline levels within 4 ms. Half widths of the pulses were between 0.5 and 2 ms.

### Procedure for dark adaptation experiments

In order to achieve a complete regeneration of the pigment in the photoreceptors, the subject spent 25 min in absolute darkness before the beginning of the experiment. Preliminary measurements of detection thresholds for luminous stimuli over this time period confirmed that subjects were fully dark-adapted after this time.

### Procedure for light adaptation experiments

Dark adaptation was prevented by repeatedly illuminating the room in between blocks of 10 experimental trials.

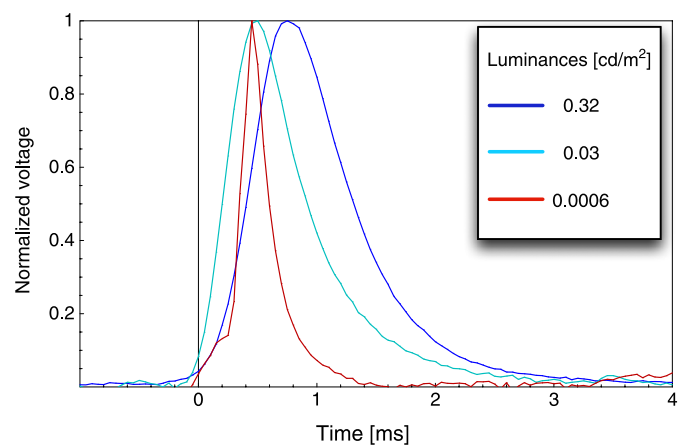


Figure 1. Photocell recording of the luminance time course on the monitor screen.

Experiments began with the room lights switched on for 210 s. Then, the room lights were extinguished and a first block of 10 trials commenced. Before each following block of 10 trials there was an additional light phase of 90 s. After each light phase there was a delay of 12 s, in which the room was completely dark before the fixation point appeared and a block of 10 trials began. An experimental session consisted of five blocks. Subjects completed multiple experimental sessions over several days.

### Threshold estimation and choice of stimulus luminances for main experiment

Individual detection thresholds of the subjects were estimated with the method of constant stimuli using 25 luminance levels (0.0001 to 0.46  $\text{cd/m}^2$ ). Each luminance level was tested five times. Different luminance levels were presented in pseudo-randomized order. The stimulus was a vertical bar of  $0.5^\circ \times 28.5^\circ$ . It was presented for one monitor frame (8 ms) at  $20^\circ$  in the visual periphery. Subjects fixated within a central area ( $3^\circ$  in diameter) and pressed a key when they felt ready for a trial. In case of successful fixation, the stimulus was flashed in the periphery, and the subject indicated visibility of the stimulus (yes/no) with a button press. An acoustic error signal was given when gaze was outside the  $3 \times 3^\circ$  fixation area, and the subject was required to re-fixate before the trial commenced.

Thresholds were derived from the 75% correct value of Weibull function fits to the response data of the subjects in the light-adapted and the dark-adapted states. Thresholds were very similar across subjects (Figure 2). We therefore used three fixed luminance values for the main experiment. Near-threshold luminance for the dark-adapted state was 0.0006  $\text{cd/m}^2$ . Near-threshold luminance for the light-adapted state was 0.03  $\text{cd/m}^2$ . This value was also used as

above-threshold luminance for the dark-adapted state. Above-threshold luminance for the light-adapted state was 0.32  $\text{cd/m}^2$ .

Luminance thresholds were measured at  $20^\circ$ , and this value was used for stimuli presented between  $5^\circ$  and  $35^\circ$ . To test for possible changes of luminance thresholds with eccentricity, we measured the dependence of the threshold on eccentricity in one representative subject (KA). In the light-adapted state, thresholds for the four eccentricities varied between 0.32 and 0.36  $\text{cd/m}^2$ . In the dark-adapted state, the threshold was 0.001  $\text{cd/m}^2$  at three positions and 0.002  $\text{cd/m}^2$  at the most eccentric position. The difference between these two values was at the limit of our measuring ability. The change from 0.001 to 0.002  $\text{cd/m}^2$  was thus a quantization problem. For both conditions, we thus found that the thresholds were similar enough over eccentricities for using a single stimulus luminance.

### Main experiments

The sequence of events in a single trial is shown in Figure 3. Each trial began with the appearance of the fixation point, which was visible for a randomly chosen period between 1000 and 2000 ms. The fixation point was located  $10^\circ$  on the left of the sagittal plane and served as the center of the coordinate system for the stimulus description. All further locations on the screen will be described relative to the fixation point. When the fixation point disappeared the saccadic target was shown for 50 ms,  $20^\circ$  to the right of the fixation point. The saccade target appeared immediately after the fixation point was extinguished. The subject executed a saccade from the fixation point to the saccade target as quickly as possible. At a random time within 300 ms after target offset, a luminous bar was flashed for one monitor frame (8 ms). The bar could appear at one of four different spatial

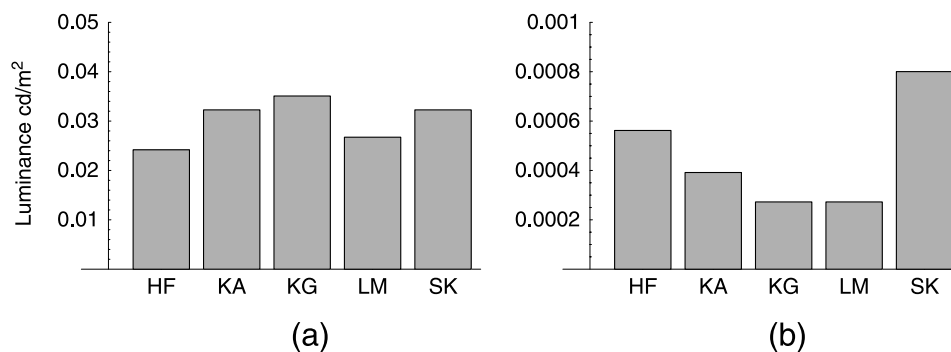


Figure 2. Detection thresholds of the subjects for luminous bars presented  $20^\circ$  in the periphery in light-adapted (a) and dark-adapted (b) state. Luminance values for the stimuli in the main experiment were derived from these threshold measurements. For the light-adapted condition, we used 0.03  $\text{cd/m}^2$  as the near-threshold stimulus and 0.32  $\text{cd/m}^2$  as the above-threshold stimulus. For the dark-adapted condition, we used 0.0006  $\text{cd/m}^2$  as the near-threshold stimulus and 0.03  $\text{cd/m}^2$  as the above-threshold stimulus.

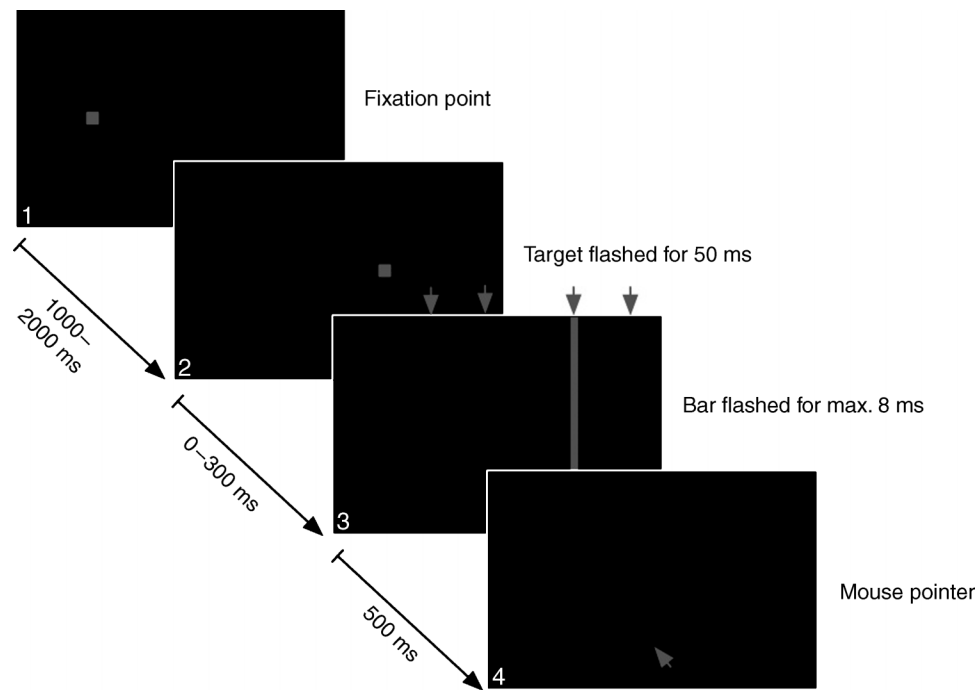


Figure 3. Stimuli and procedure. At the beginning of each trial, the subject fixated a fixation point  $10^\circ$  left of the sagittal plane. After a randomized time between 1000 and 2000 ms, the fixation point disappeared and the saccade target appeared for 50 ms  $20^\circ$  to the right of fixation. The subject performed a saccade towards the target as fast as possible. At a random time within 300 ms after target offset, a vertical bar was flashed at one of four possible positions ( $5^\circ$ ,  $12.5^\circ$ ,  $27.5^\circ$ ,  $35^\circ$ ) for one monitor frame (8 ms). Five hundred milliseconds after the bar presentation, the mouse pointer appeared in which the subjects pointed at the perceived bar position.

positions distributed equidistantly around the saccade target ( $5^\circ$ ,  $12.5^\circ$ ,  $27.5^\circ$ , and  $35^\circ$ ). The bar position as well as its time of appearance were pseudo-randomized. Because of the visible persistence of the saccade target, which can last up to 300 ms, the flash might be seen along with the persistence of the saccadic target. Five hundred milliseconds after the stimulus presentation, a mouse pointer appeared on the screen ( $0.039 \text{ cd/m}^2$ ). The subject indicated the perceived position of the bar by a mouse click at the corresponding horizontal position on the black screen. If no stimulus was perceived, the subject clicked at the left edge of the screen. These trials were discarded from further evaluation. The next trial automatically began after the response of the last event.

## Data analysis

Data were analyzed in Mathematica 5.1 (Wolfram Research). The onset of a saccade was defined as the first of three sequential eye position samples with a velocity above  $22^\circ/\text{s}$  and an acceleration above  $3800^\circ/\text{s}^2$ . Trials in which the latency was not between 100 and 300 ms or in which the eye landed more than  $4^\circ$  away from the saccade

target were omitted from further analysis. The total number of trials that were included in the analysis is listed for each subject and condition (see Figures 4–7).

## Results

Figures 4 and 5 show the apparent positions of peri-saccadically flashed bars with luminance high above threshold (Figure 4) and near threshold (Figure 5) in the light-adapted state for the five individual subjects.

In each panel, the perceived positions of the four bars (identified by colors) are plotted as a function of time relative to saccade onset. The four veridical bar positions are represented by short lines on the left and right of every panel. The short gray line on the left at  $20^\circ$  indicates the position of the saccade target. The position of the long gray line gives the average landing position of the eye. The width of the line corresponds to the standard error of the landing position and indicates the accuracy of the saccade. The yellow rectangle represents the mean duration of the saccade. The colored symbols give the perceived position for a particular bar at a particular

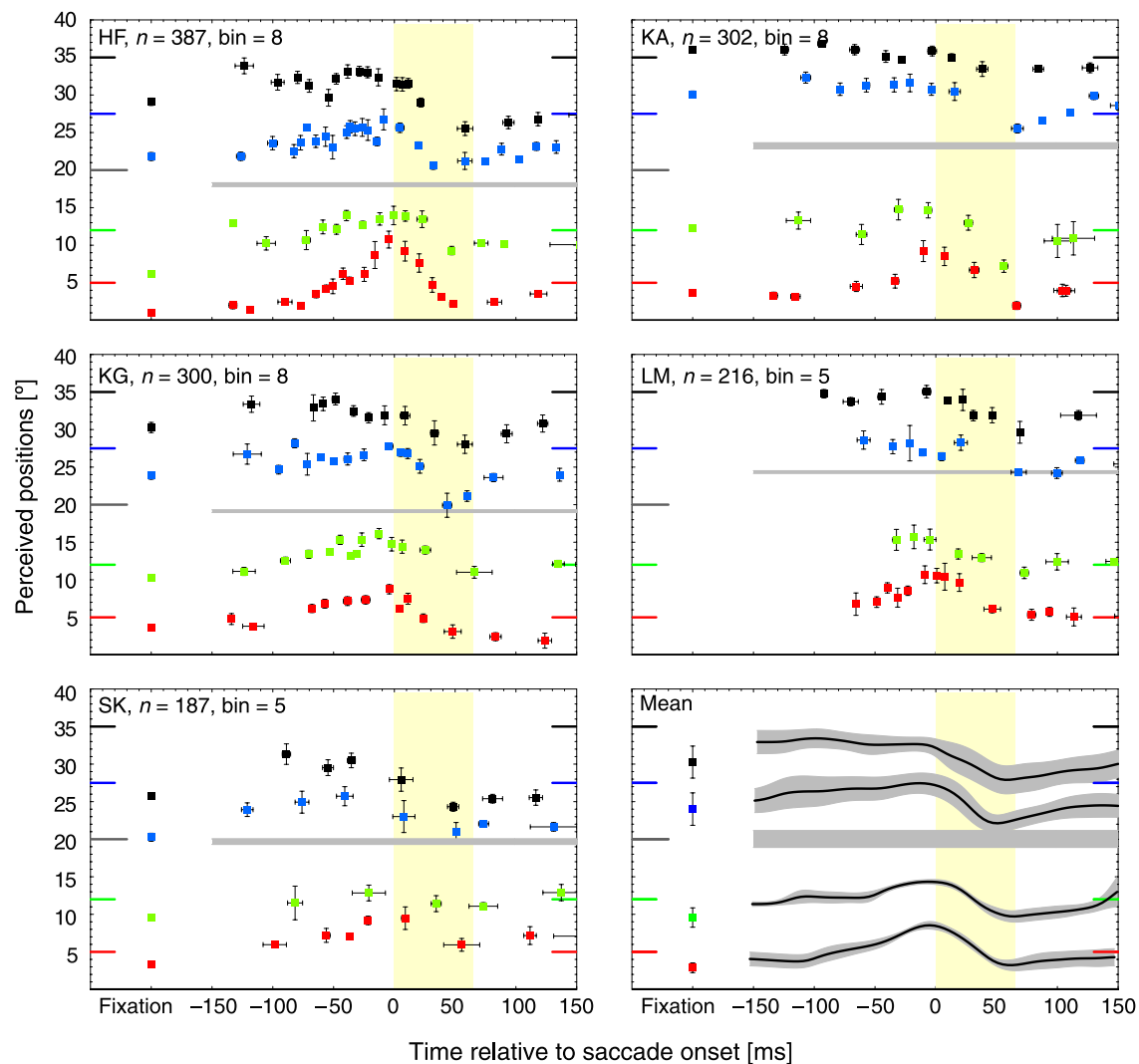


Figure 4. Apparent positions for above-threshold stimuli in light-adapted subjects as a function of presentation time relative to saccade onset. Symbols present means and standard errors over 8 or 5 data points collected near a particular presentation time. Colors correspond to the four true bar position, which are indicated by short lines on edges of each panel. The long gray line gives the average landing position of the eye; its width the standard error of the landing position. The yellow rectangle represents the mean duration of the saccade. The curves in the lower right panel show the means (dark lines) and standard errors (gray areas) across subjects.

presentation time relative to saccade onset. Each symbol is the mean over 8 or 5 data points collected near that time point. Error bars depict standard errors over that sample bin. The bin width (8 or 5) and the total number of data points in the plot are indicated in the legend for each subject. The four data points on the left of each panel of subjects HF, KA, KG, and SK give the mean perceived location (and its standard error) during fixation, as measured in separate control trials. The lower right panel depicts the mean across all five subjects. The curves show interpolated values for the perceived bar positions. The dark line of each curve plots the perceived position of flashes at one particular stimulus position over time, calculated from a running average of each subject over the

single trial data with a moving Gaussian window of 20 ms width. The gray area surrounding the line gives the standard error over the five subjects.

Mislocalization is much larger for the near-threshold stimuli (Figure 5) than for the stimuli with luminance well above threshold (Figure 4). For both luminances, the magnitude of mislocalization varies with stimulus position, as the flashes at positions 5° (red) and 12.5° (green) show more shift in saccade direction than the flashes at positions 27.5° (blue) and 35° (black). For luminance well above threshold (Figure 4), flashes at positions 27.5° (blue) and 35° (black) show a backwards shift late during the saccade. For near-threshold stimuli (Figure 5), flashes presented at positions 27.5° are shifted in the direction of

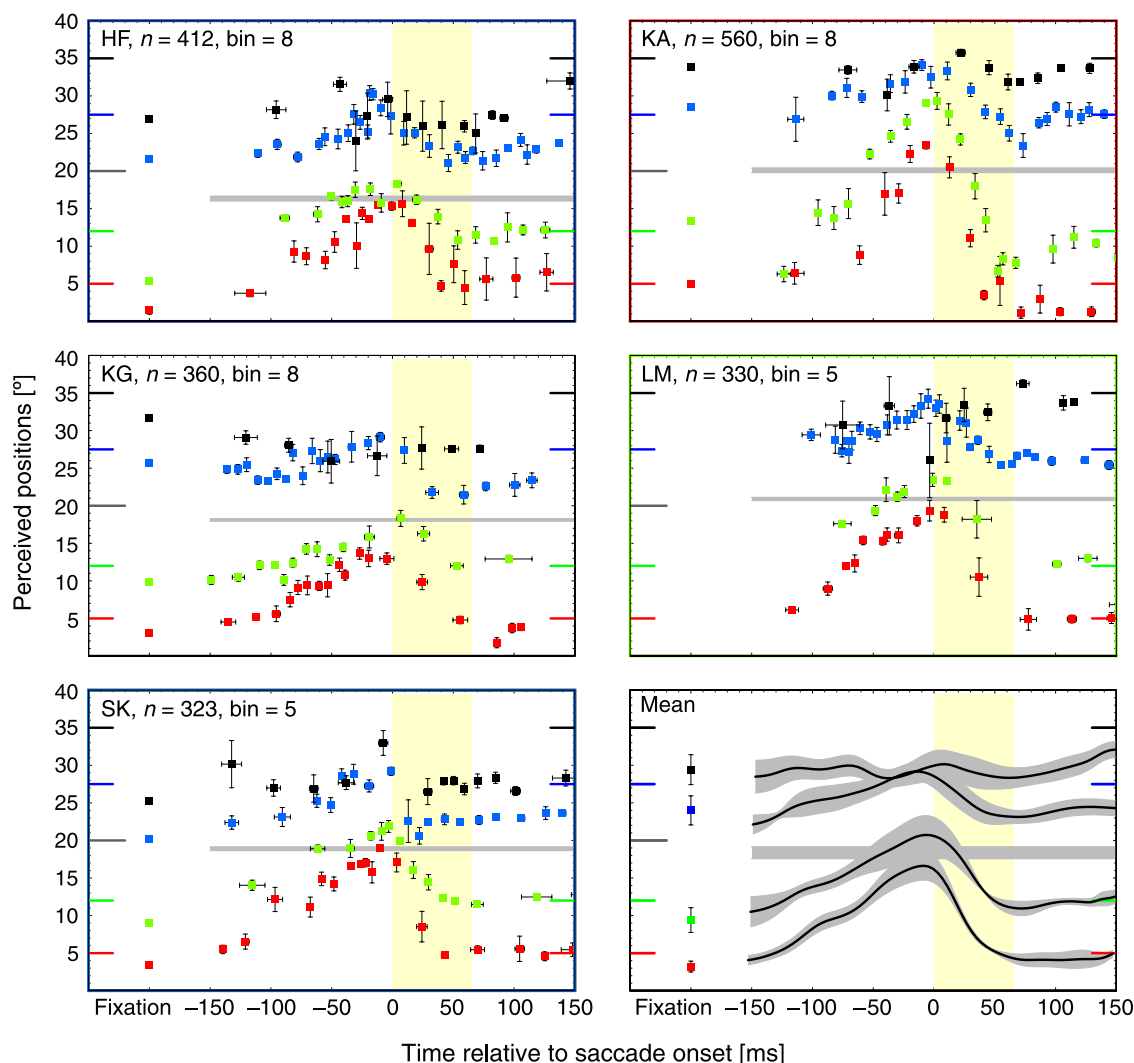


Figure 5. Apparent positions for near-threshold stimuli in light-adapted subjects as a function of presentation time relative to saccade onset. Symbols present means and standard errors over 8 or 5 data points collected near a particular presentation time. Colors correspond to the four true bar position, which are indicated by short lines on edges of each panel. The long gray line gives the average landing position of the eye; its width the standard error of the landing position. The yellow rectangle represents the mean duration of the saccade. The curves in the lower right panel show the means (dark lines) and standard errors (gray areas) across subjects.

the saccade although not as much as the flashes at positions  $5^\circ$  and  $12.5^\circ$ . Flashes at position  $35^\circ$  do not show a consistent pattern of mislocalization around saccade onset.

In many cases, flashes at position  $35^\circ$  show an overall bias towards lower eccentricities. This bias can also be observed for presentation times long before or after the saccade at other bar positions. Such a bias can be seen in many previous peri-saccadic localization studies (Awater & Lappe, 2006; Burr, Morrone, & Ross, 2001; Dassonville et al., 1992; Michels & Lappe, 2004; Ostendorf, Fischer, Gaymard, & Ploner, 2006) as well as in studies that investigated flash localization during fixation (Eggert, Ditterich, & Straube, 2001; Müsseler, van der Heijden,

Mahmud, Deubel, & Ertsey, 1999; Ostendorf et al., 2006; Sheth & Shimojo, 2001). Its strength differs between subjects and conditions, which may explain why some studies have not observed a bias (e.g., Morrone et al., 1997; Ross et al., 1997). In control experiments in four of our subjects, we measured localization bias during fixation (left column in the figure panels). The controls show that the bias occurs also during fixation and that it is thus not related to the occurrence of the saccade or to peri-saccadic processes.

Figure 6 shows the apparent positions of peri-saccadically flashed bars with luminance high above threshold in the dark-adapted state. The stimulus luminance is identical to the one in Figure 5. However, in the dark-adapted

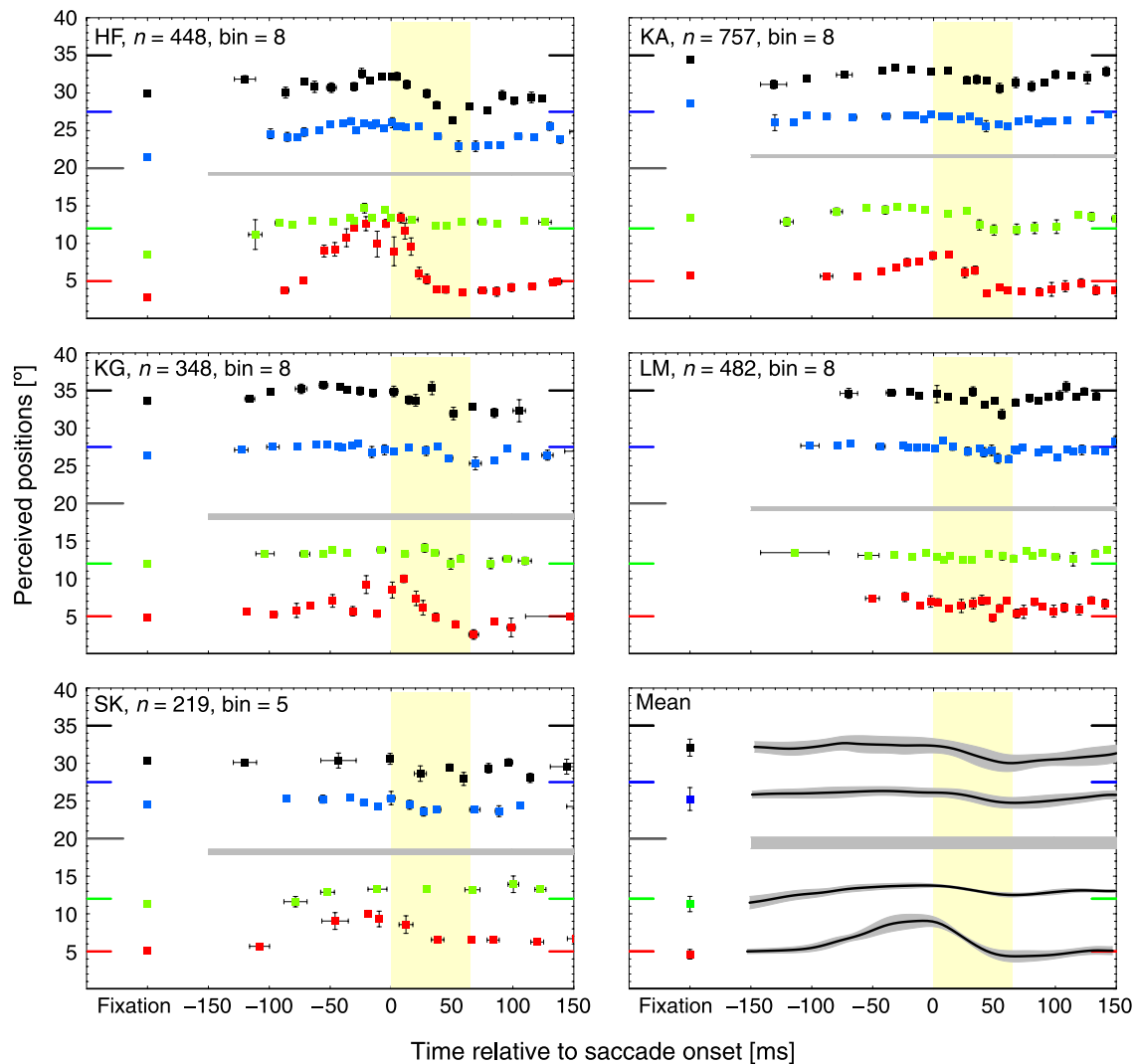


Figure 6. Apparent positions for above-threshold stimuli in dark-adapted subjects. Symbols present means and standard errors over 8 or 5 data points collected near a particular presentation time relative to saccade onset. Colors correspond to the four true bar position, which are indicated by short lines on edges of each panel. The long gray line gives the average landing position of the eye; its width the standard error of the landing position. The yellow rectangle represents the mean duration of the saccade. The curves in the lower right panel show the means (dark lines) and standard errors (gray areas) across subjects.

state, the same luminance now results in only a small mislocalization in saccade direction at the  $5^\circ$  position.

Figure 7 shows the apparent positions of peri-saccadically flashed bars with luminance near threshold in the dark-adapted state. There is a clear shift in saccade direction for the stimulus positions  $5^\circ$  and  $12.5^\circ$  and a slight shift for the  $27.5^\circ$  position in the mean data. The most eccentric position ( $35^\circ$ ) appears shifted a bit against saccade direction in subjects KG and LM.

## Discussion

The pattern of peri-saccadic mislocalization in the dark is influenced by the intensity of the stimulus and the

adaptation state of the subject. When stimulus intensity is close to detection threshold, the apparent position of the stimulus shows large mislocalization. When stimulus intensity is far above threshold, this mislocalization is very weak.

Dark adaptation influences the pattern of peri-saccadic mislocalization because it increases the luminance sensitivity of the photoreceptors and lowers the intensity threshold for stimulus detection. Hence, stimuli that are near threshold in the light-adapted condition are well above threshold in the dark-adapted state. These stimuli are only weakly mislocalized. However, when stimulus intensity is lowered to near-threshold in the dark-adapted state, mislocalization is seen for these stimuli in a similar way as for near-threshold stimuli in the light-adapted state. Therefore, we conclude that the stimulus intensity

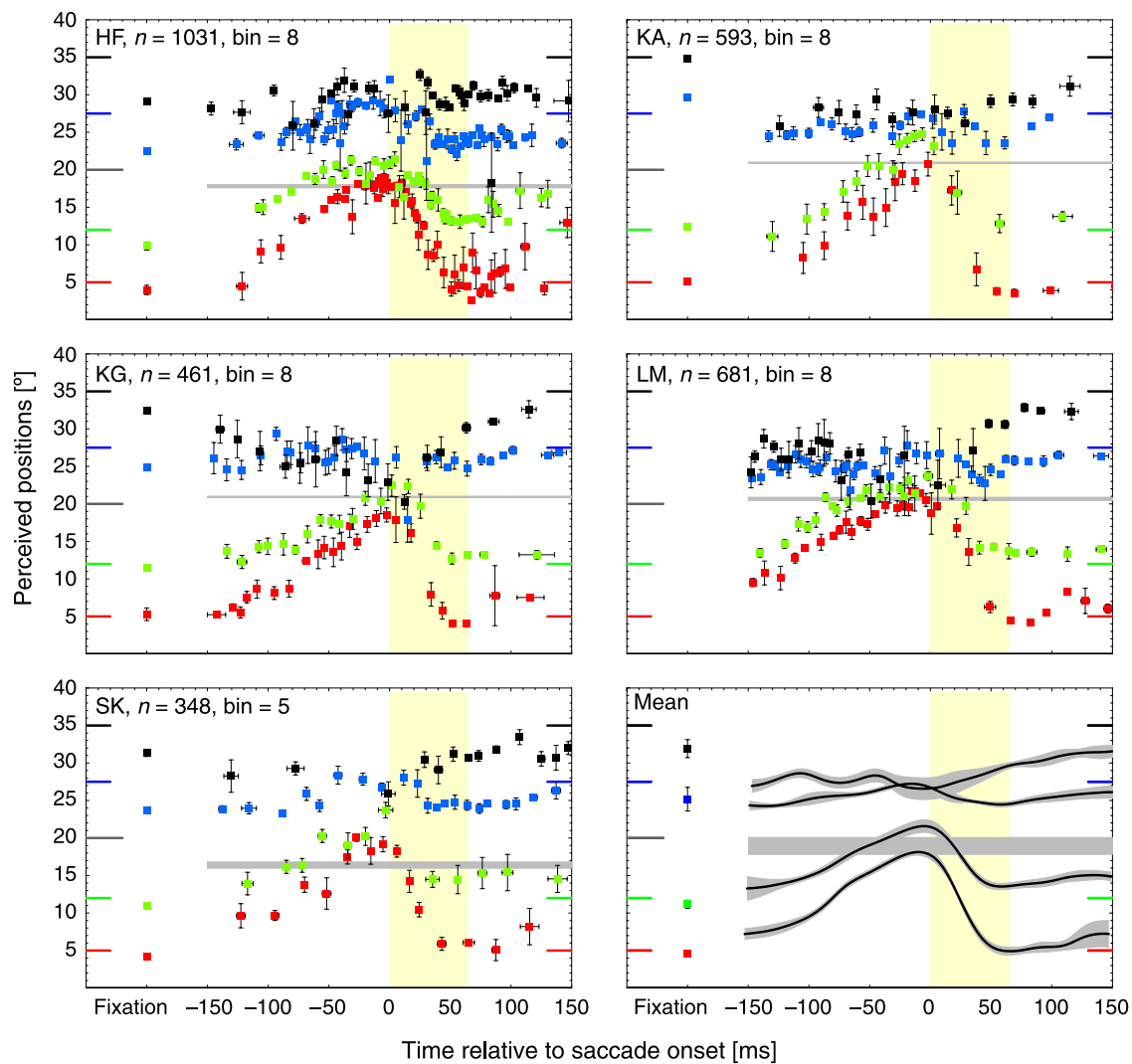


Figure 7. Apparent positions for near-threshold stimuli in dark-adapted subjects. Symbols present means and standard errors over 8 or 5 data points collected near a particular presentation time relative to saccade onset. Colors correspond to the four true bar positions, which are indicated by short lines on the edges of each panel. The long gray line gives the average landing position of the eye; its width the standard error of the landing position. The yellow rectangle represents the mean duration of the saccade. The curves in the lower right panel show the means (dark lines) and standard errors (gray areas) across subjects.

relative to threshold is the main factor in these experiments.

The mislocalization in the near-threshold condition was very similar for dark-adapted and light-adapted subjects. The mislocalization in the above-threshold condition was somewhat stronger in the light-adapted measurements (Figure 4) than in the dark-adapted measurements (Figure 6). However, the ratio between above-threshold and near-threshold luminance was much higher for the dark-adapted condition than for the light-adapted (approximately 50:1 versus 10:1). The difference between the two adaptation conditions may be explained by the different intensity-to-threshold ratios of the stimuli.

The response of the visual system to brief luminance stimuli, the impulse response function, changes with adaptation level (Ikeda, 1986). For the light-adapted eye,

the impulse response function is diphasic, with a quick excitatory and a delayed inhibitory component. The excitatory response lasts for about 50 ms. In the dark-adapted eye, the temporal impulse response function to luminance is monophasic and longer lasting (up to 150 ms) (Hallett, 1969; Ikeda, 1986; Roufs, 1973; Swanson, Ueno, Smith, & Pokorny, 1987), similar to the impulse response function to chromatic stimuli in the light-adapted eye (Burr & Morrone, 1993). However, a change in the temporal properties of the impulse response function is unlikely to be the source of the variation in our data. The impulse response function is monophasic and long lasting for both stimulus luminances in our dark-adapted condition (Hallett, 1969; Ikeda, 1986; Roufs, 1973; Swanson et al., 1987). Yet the mislocalization strength is very different for the two luminances.



The time course of mislocalization is virtually identical in both adaptation states. In the near-threshold conditions, mislocalization begins about 100 ms before the saccade, peaks at saccade onset, and ends at around 50 ms after saccade onset, i.e., just before the end of the saccade. This is the typical time course obtained in many studies of peri-saccadic mislocalization (Dassonville et al., 1992; Honda, 1989, 1991, 1993; Lappe et al., 2000; Morrone et al., 1997). Thus, although dark adaptation is known to affect perceived timing and duration of stimuli this does not affect the time course of peri-saccadic mislocalization. This also argues against the change in the temporal impulse response function as the origin of mislocalization.

The mislocalization of near-threshold stimuli is not uniform across the visual field. Positions between the fixation point and the saccade target are strongly shifted in saccade direction, whereas positions beyond the saccade target show little or no shift in saccade direction. Therefore, around saccade onset, the spatial separation between the apparent positions of the four stimuli is much smaller than their true spatial separation. This is similar to peri-saccadic compression. However, the center of mass of the four positions seems to be shifted beyond the saccade target. This is atypical for peri-saccadic compression. It is also important to note that the most eccentric flash position does not show any variation over time but is localized at less eccentric values throughout the tested time range.

The dependence of mislocalization on luminance in the dark is reminiscent of the dependence of peri-saccadic compression on contrast (Michels & Lappe, 2004). In both cases, mislocalization becomes larger when stimulus visibility decreases. The dependence on contrast is predicted by a neurocomputational model in which feedback of the oculomotor signal of the saccade to visual areas modifies the population response to the stimulus such that its apparent location is shifted towards the saccade target position (Hamker, Zirnsak, Calow, & Lappe, 2006). In this model, spatial position is calculated from the population response elicited by a stimulus. A spatially non-uniform oculomotor feedback signal centered at the saccade target changes the gain of neurons. As a result, the peri-saccadic population response is distorted, and the stimulus is perceived offset from its true position towards the saccade target. The gain increase acts on the input to the neuron and depends on the firing rate within the neural population. Thus, for moderate inputs near threshold the gain increase is large since the firing rate in the population is low. For strong inputs that by themselves lead to nearly saturation responses, the gain change is small. Therefore, near-threshold stimuli show a large amount of mislocalization whereas strong stimuli show little mislocalization. This might explain the dependence of mislocalization on luminance and adaptation state. In a particular adaptation state, low-luminance stimuli elicit lower responses than high luminance stimuli. A stimulus of a particular luminance elicits higher responses in the dark-adapted state than in the light-adapted state.

Pola (2004) proposed a model in which the latency and perceptual duration of the stimulus are important factors for the peri-saccadic shift in darkness. Since latency and perceptual duration of a stimulus vary with luminance and with adaptation state, this model may also predict a variation of the magnitude of peri-saccadic shift with stimulus luminance. However, the non-uniformity of the mislocalization in our near-threshold conditions can be reconciled with this model only if the luminance dependence in the model varies across the visual field.

The variation of the mislocalization over the visual field in the near-threshold conditions may be described as a combination of peri-saccadic shift and compression. Peri-saccadic shift has been observed under many circumstances (Dassonville et al., 1992; Honda, 1989, 1991; Lappe et al., 2000; Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995) and is independent of contrast (Michels & Lappe, 2004). Compression has so far been observed only under conditions including a visual background (Awater & Lappe, 2006; Bischof & Kramer, 1968; Lappe et al., 2000; Morrone et al., 1997; Ross et al., 1997). In particular, Lappe et al. (2000) have compared the strength of compression in darkness, and when a ruler with visual reference information about the target position was presented on an otherwise dark screen. Compression was weak in darkness and larger when the ruler was available after the saccade. Since the stimuli in that study were of high luminance, the data in darkness are not in conflict with the present data. The present data extend the investigations to low luminance stimuli and show that these stimuli can give rise to some compression in darkness (e.g. subjects KG and LM in Figure 7). This is a new finding. However, in the earlier study compression occurred for high contrast stimuli in the presence of visual references. This cannot be explained by differences in contrast or luminance since compression also occurred when the references were only presented after the saccade. Thus, we have to conclude that stimulus strength (i.e. luminance (present data) or contrast (Michels & Lappe, 2004)) modulates the strength of compression, and that post-saccadic visual references also modulate the strength of compression. In this respect, it is important to note furthermore that the overall strength of compression in Lappe et al. (2000) even in the condition with visual references was low compared to the compression strength that can be obtained under low contrast conditions with visual references (cf. Michels & Lappe, 2004; Morrone et al., 1997).

The dependence on stimulus strength and visual references may be explained by two successive processes: First, a compression of distance to the target in a retinotopic map (the strength of which depends on stimulus strength); and second, a transformation from retinotopic coordinates to exocentric coordinates (Awater & Lappe, 2006). First, the visual system gathers information about the retinal position of the flash, the retinal position of the saccade target, and the retinal distance of

the flash from the target before the saccade begins. The distance of the flash from the target is compressed by the action of the oculomotor feedback signal on the neuronal population response as described above. Thereafter, compression is manifested in retinal coordinates. In order for this compression to be reflected in manual responses, retinal coordinates have to be transformed to exocentric coordinates in the second step. This transformation may use extraretinal eye position signals (Binda, Bruno, Burr, & Morrone, 2007; Dassonville et al., 1992; Honda, 1991; Matin, Matin, & Pearce, 1969; Pola, 2004), memory of the saccade target (Matin et al., 1969), or visual reference information about the saccade target position in the post-saccadic image together with prior assumptions about the stability of the visual world (Deubel, Bridgeman, & Schneider, 2004; McConkie & Currie, 1996; Niemeier, Crawford, & Tweed, 2003). The outcome of this transformation depends on the availability of these signals (for instance, visual reference information does not exist in the dark) and on the weights that the transformation process puts on the different signals (Binda et al., 2007; Niemeier et al., 2003). Quantitative predictions are difficult without knowing the full set of weights but some qualitative speculations may be made. If post-saccadic visual reference information about the target position is available, this information is used preferentially to locate the target (Deubel et al., 2004; McConkie & Currie, 1996). The flash is then located at the compressed distance from the target. This is consistent with the dependence of the occurrence of compression on the presence of post-saccadic visual references (Awater & Lappe, 2006; Lappe et al., 2000). When visual references are not available after the saccade (like in the current study), the transformation may put different weights on the saccade target and flash positions depending on their respective visibility. We may speculate that when the flash is strong and salient localization commences with determining the location of the flash from extraretinal signals (Binda et al., 2007; Honda, 1991; Matin et al., 1969; Pola, 2004). This is consistent with the above-threshold conditions in the current experiments and with many previous experiments conducted with bright, salient peri-saccadic flashes in the dark (Dassonville et al., 1992; Honda, 1989, 1991; Lappe et al., 2000; Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). When the flash is less salient, localization may instead commence by reconstructing the saccade target position from extraretinal signals and then estimating the location of the flash from its compressed distance to the target. Consequently, the apparent position of the flash should become compressed towards the saccade target. However, since localization from extraretinal signals is subject to the peri-saccadic shift, the reconstruction should be shifted somewhat in saccade direction around saccade onset. Hence, the compression should be centered on a position that is physically shifted a bit further than the saccade target. This is consistent with the results of the near-threshold condition.

The dependence of peri-saccadic mislocalization on stimulus luminance may also explain how the mislocalization is related to the duration of the stimulus. According to Bloch's law, perceived intensity of brief stimuli is the product of stimulus duration and luminance. It would be interesting to see how luminance can be traded for duration in peri-saccadic mislocalization.

## Acknowledgments

This work was supported by the German Science Foundation *DFG LA-952/3* and the German Federal Ministry of Education and Research project *Visuo-spatial cognition*.

Commercial relationships: none.

Corresponding author: Markus Lappe.

Email: mlappe@psy.uni-muenster.de.

Address: Psychological Institute II, Westfaelien Wilhelms University Muenster, Fliednerstrasse 21, 48149 Muenster, Germany.

## References

- Awater, H., & Lappe, M. (2006). Mislocalization of perceived saccade target position induced by peri-saccadic visual stimulation. *Journal of Neuroscience*, 26, 12–20. [[PubMed](#)] [[Article](#)]
- Binda, P., Bruno, A., Burr, D. C., & Morrone, M. C. (2007). Fusion of visual and auditory stimuli during saccades: A Bayesian explanation for perisaccadic distortions. *Journal of Neuroscience*, 27, 8525–8532. [[PubMed](#)]
- Bischof, N., & Kramer, E. (1968). Investigations and considerations of directional perception during voluntary saccadic eye movements. *Psychologische Forschung*, 32, 185–218. [[PubMed](#)]
- Burr, D. C., & Morrone, M. C. (1993). Impulse-response functions for chromatic and achromatic stimuli. *Journal of the Optical Society of America A*, 10, 1706–1713.
- Burr, D. C., Morrone, M. C., & Ross, J. (2001). Separate visual representations for perception and action revealed by saccadic eye movements. *Current Biology*, 11, 798–802. [[PubMed](#)] [[Article](#)]
- Dassonville, P., Schlag, J., & Schlag-Rey, M. (1992). Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Visual Neuroscience*, 9, 261–269. [[PubMed](#)]

- Dassonville, P., Schlag, J., & Schlag-Rey, M. (1995). The use of egocentric and exocentric location cues in saccadic programming. *Vision Research*, *35*, 2191–2199. [PubMed]
- Deubel, H., Bridgeman, B., & Schneider, W. X. (2004). Different effects of eyelid blinks and target blanking on saccadic suppression of displacement. *Perception & Psychophysics*, *66*, 772–778. [PubMed] [Article]
- Eggert, T., Ditterich, J., & Straube, A. (2001). Mislocalization of peripheral targets during fixation. *Vision Research*, *41*, 343–352. [PubMed]
- Hallett, P. E. (1969). Impulse functions for human rod vision. *The Journal of Physiology*, *202*, 379–402. [PubMed] [Article]
- Hamker, F. H., Zirnsak, M., Calow, D., & Lappe, M. (2006). The perisaccadic compression of visual space—What may it have to do with spatial attention [Abstract]? *Journal of Vision*, *6*(6):105, 105a, <http://journalofvision.org/6/6/105/>, doi:10.1167/6.6.105.
- Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics*, *45*, 162–174. [PubMed]
- Honda, H. (1991). The time course of visual mislocalization and of extraretinal eye position signals at the time of vertical saccades. *Vision Research*, *31*, 1915–1921. [PubMed]
- Honda, H. (1993). Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. *Vision Research*, *33*, 709–716. [PubMed]
- Ikeda, M. (1986). Temporal impulse response. *Vision Research*, *26*, 1431–1440. [PubMed]
- Kaiser, M., & Lappe, M. (2004). Perisaccadic mislocalization orthogonal to saccade direction. *Neuron*, *41*, 293–300. [PubMed] [Article]
- Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, *403*, 892–895. [PubMed]
- Matin, L., Matin, E., & Pearce, D. G. (1969). Visual perception of direction when voluntary saccades occur: I. relation of visual directions of a fixation target extinguished before a saccade to a subsequent test flash presented during the saccade. *Perception & Psychophysics*, *5*, 65–80.
- Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science*, *148*, 1485–1488. [PubMed]
- McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 563–581. [PubMed]
- Michels, L., & Lappe, M. (2004). Contrast dependency of saccadic compression and suppression. *Vision Research*, *44*, 2327–2336. [PubMed]
- Morrone, M. C., Ross, J., & Burr, D. C. (1997). Apparent position of visual targets during real and simulated saccadic eye movements. *Journal of Neuroscience*, *17*, 7941–7953. [PubMed] [Article]
- Müsseler, J., van der Heijden, A. H., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perception & Psychophysics*, *61*, 1646–1661. [PubMed]
- Niemeier, M., Crawford, J. D., & Tweed, D. B. (2003). Optimal transsaccadic integration explains distorted spatial perception. *Nature*, *422*, 76–80. [PubMed]
- Ostendorf, F., Fischer, C., Gaymard, B., & Ploner, C. J. (2006). Perisaccadic mislocalization without saccadic eye movements. *Neuroscience*, *137*, 737–745. [PubMed]
- Pola, J. (2004). Models of the mechanism underlying perceived location of a perisaccadic flash. *Vision Research*, *44*, 2799–2813. [PubMed]
- Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*, *386*, 598–601. [PubMed]
- Roufs, J. A. (1973). Dynamic properties of vision. III. Twin flashes, single flashes and flicker fusion. *Vision Research*, *13*, 309–323. [PubMed]
- Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research*, *35*, 2347–2357. [PubMed]
- Sheth, B. R., & Shimojo, S. (2001). Compression of space in visual memory. *Vision Research*, *41*, 329–341. [PubMed]
- Swanson, W. H., Ueno, T., Smith, V. C., & Pokorny, J. (1987). Temporal modulation sensitivity and pulse-detection thresholds for chromatic and luminance perturbations. *Journal of the Optical Society of America A, Optics and Image Science*, *4*, 1992–2005. [PubMed]