



Localization of visual targets during optokinetic eye movements

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Abstract

We investigated localization of brief visual targets during reflexive eye movements (optokinetic nystagmus). Subjects mislocalized these targets in the direction of the slow eye movement. This error decreased shortly before a saccade and temporarily increased afterwards. The pattern of mislocalization differs markedly from mislocalization during voluntary eye movements in the presence of visual references, but (spatially) resembles mislocalization during voluntary eye movements in darkness. Because neither reflexive eye movements nor voluntary eye movements in darkness have explicit (visual) goals, these data support the view that visual goals support perceptual stability as an important link between pre- and post-saccadic scenes.

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1. Introduction

Eye movements challenge visual processing. While the image of external objects moves across the retina during such movements, we perceive the outer world as being stable. Yet, it appears, that this perceptual stability is not complete. Several studies have shown that spatial processing in the temporal vicinity of voluntary eye movements is not veridical. During smooth pursuit eye movements the perceived location of briefly flashed visual stimuli is shifted in the direction of the pursuit (Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979; Mateeff, Yakimoff, & Dimitrov, 1981; Rotman, Brenner, & Smeets, 2004, 2005; van Beers, Wolpert, & Haggard, 2001). This mislocalization is observed mainly in one visual hemifield, i.e. the one the fovea is heading for (van Beers et al., 2001). In addition, the perceptual error increases with increasing retinal eccentricity.

During visually guided saccades different mislocalization patterns can be observed depending on the exact experimental conditions. In total darkness a temporally biphasic

perisaccadic mislocalization pattern has been described (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Honda, 1989). Until the start of the eye movement all positions are perceptually shifted in the direction of the saccade. The maximum displacement is typically reached at the onset of the saccade. This shift is followed by a displacement against saccade direction. Approximately 100 ms after the end of the saccade perception is again veridical. This spatio-temporal pattern is completely changed when saccades are performed in the presence of visual references. In such case all perceived locations are shifted towards the endpoint of the saccade, leading to a perceptual compression of space (Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997). The strength of this mislocalization is related to the length of the saccade: the longer the saccade vector the larger the localization error (Kaiser & Lappe, 2004; Morrone, Ross, & Burr, 1997).

Both pursuit related and perisaccadic mislocalization have typically been interpreted as a mismatch between the visual system's representation of the eye position and the actual position of the eye (Schlag & Schlag-Rey, 2002, saccades: Dassonville, Schlag, & Schlag-Rey, 1992; Pola, 2004; pursuit: Brenner, Smeets, & van den Berg, 2001; van Beers et al., 2001). In addition for both types of eye movements

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visual mechanisms have been shown to influence localization (Awater & Lappe, 2006; Lappe et al., 2000; Rotman et al., 2004). In other words, these studies show the imperfections of the mechanisms of perceptual stability (Bremmer & Krekelberg, 2003).

Both visually guided saccades and smooth pursuit are voluntary eye movements, which are controlled to a large extent in a number of cortical areas as shown by functional imaging studies in humans (saccades: Corbetta et al., 1998; Kimmig et al., 2001; Konen, Kleiser, Wittsack, Bremmer, & Seitz, 2004, pursuit: Konen, Kleiser, Seitz, & Bremmer, 2005; Nagel et al., 2006; Petit & Haxby, 1999) and single cell recordings in non-human primates (saccades: Barash, Bracewell, Fogassi, Gnadt, & Andersen, 1991a, 1991b; Schall, 1991; pursuit: Bremmer, Ilg, Thiele, Distler, & Hoffmann, 1997; Ilg & Thier, 2003; Newsome, Wurtz, & Komatsu, 1988. For review see: Ilg, 1997; Thier & Ilg, 2005). Reflexive eye movements such as the optokinetic nystagmus (OKN), on the other hand, are phylogenetically much older (Carpenter, 1988). The OKN mainly subserves the stabilization of the whole image on the retina e.g. during head movements. The OKN is an alternation of slow-phases in the direction of the stimulus motion and fast-phases against the direction of stimulus motion. While the fast phases are similar to saccades the slow-phases are considered to be different from smooth pursuit during late OKN while during the early phase of the OKN it is difficult to differentiate between the ocular following reflex, smooth pursuit and OKN (Leigh & Zee, 2006). One notable difference, showing that quite different motor control mechanisms are involved in the control of smooth pursuit and OKN, is the observation of an after-nystagmus. When the full-field stimulus that induces an OKN is turned off, leaving the subject in darkness, OKN-like eye movements with decreasing amplitude are observed. Such an after-effect, called an optokinetic after-nystagmus, is not observed for smooth pursuit eye movements. At the subcortical level, the OKN is mainly controlled by the Nucleus of the Optic Tract (NOT-DTN) (Ilg & Hoffmann, 1991, 1996).

Clearly, the issues that the visual system has to deal with during OKN are quite similar to those during voluntary eye movements. To generate a stable spatial percept, the eye-movements have to be accounted for in some fashion. Given that the motor control of the OKN is quite different from that of the voluntary eye movements (see Section 4), we reasoned that further insight into the mechanisms of perceptual stability could be gained by investigating localization during these reflexive eye movements.

Mimicking the paradigms used to study localization during voluntary eye movements, we asked human subjects to localize briefly flashed visual targets during optokinetic eye movements. We found that, just as during smooth pursuit, flashes are mislocalized in the direction of the eye movement during the slow-phase of the OKN. Contrary to the reported findings during pursuit, mislocalization errors during OKN slow-phase did not depend on the retinal position. During the fast-phases the mislocalization was modulated in a manner that was similar to the mislocalization

during voluntary saccades in darkness: the spatial characteristics were identical, while the temporal properties of the two effects were different. In accordance with findings from Tozzi, Morrone, and Burr (2006, 2005) the dynamic error during OKN fast-phase was independent of target position.

These findings are consistent with the view that localization during fast and slow reflexive eye movements relies on similar mechanisms that operate in darkness during voluntary eye movements. Additional mechanisms that rely on the use of visual references seem to be less important during OKN. Preliminary results have been reported in abstract form (Kaminiarz, Rohe, Krekelberg, & Bremmer, 2006).

2. Methods

2.1. Subjects

Nine human subjects participated in the experiments; all had normal or corrected-to-normal visual acuity, and were experienced psychophysical observers. Seven of the subjects were naïve as to the purpose of the study. All subjects gave informed written consent and all procedures used in the present study conformed to the Declaration of Helsinki.

2.2. Stimulus presentation and eye movement recordings

Computer generated stimuli (see below) were presented on a ViewSonic P225f monitor with a spatial resolution of 1152×864 pixels and a frame rate of 100 Hz. The screen was viewed binocularly at a viewing distance of 57 cm. A fixed head position was maintained by a chin and forehead rest. In order to avoid visual reference cues the experiments were carried out in a completely dark room and the monitor casing was occluded with a black cover with a circular aperture 25° in diameter. Eye position was sampled at 500 Hz using an infrared eye tracker (EyeLink 2, SR Research Inc.). The data were stored on hard disk for offline analysis.

2.3. Visual stimuli

The background of the monitor was a homogeneous gray. On top of this background, a visual localization target (white circle, 0.5° in diameter, luminance: 74.2 cd/m^2) was flashed for 10 ms at one of five possible locations in the upper half of the visual field: $[x, y] = [\pm 5^\circ, 0^\circ], [\pm 3.5^\circ, 3.5^\circ], [0, 5^\circ]$ (See Fig. 1c).

To induce optokinetic nystagmus, a random dot pattern (RDP) consisting of black dots (size: 0.17° , luminance: $<0.1 \text{ cd/m}^2$, average number of visible dots: 205) moved horizontally in pseudorandomized order either to the left or to the right. All elements of the RDP moved coherently with a speed of 10 deg/s. A new RDP was generated for each trial.

The fixation point consisted of a white (0.35° in diameter) and black circle (0.11°) at the center of the display.

A randomized ruler was used to obtain response-bias free estimates of the perceived position of the flash. This ruler was displayed at the end of a trial only and consisted of a white line with a tick mark at every 0.5 degrees. The tick marks were always in the same position, but they were re-labeled with new random labels (between 10 and 99) every trial. This re-labeling prevented the subjects from acquiring stereotypical response strategies, which could have been induced by the limited number of target positions. Subjects entered the perceived position of the flash (the label of the nearest tick mark) on the keyboard. Offline, these labels were converted back to the appropriate spatial location.

2.4. Free viewing trials

In the 'free viewing' condition, subjects freely viewed a homogeneous gray monitor for 4000 ms. The visual target was flashed after 3500 ms.

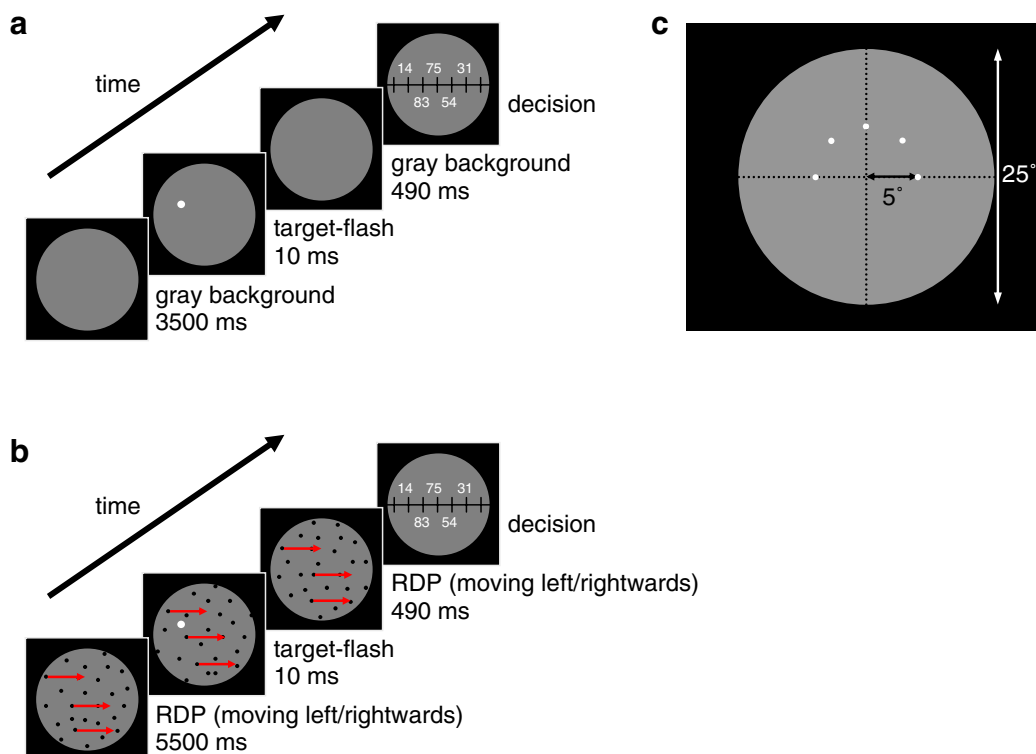


Fig. 1. Schematic illustration of the temporal sequence of a single baseline (a) or OKN (b) trial of experiment 1. During baseline measurements subjects freely viewed a homogeneous gray monitor for 4000 ms. After 3500 ms a target was flashed for 10 ms (1 frame) at one of 5 possible locations. A ruler appeared 490 ms later and subjects had to indicate which number on the ruler was closest to the perceived position of the flashed target. During each session the ruler was oriented either horizontally or vertically. During eye movements trials OKN was triggered using an RDP moving either left- or rightwards for 6000 ms. After 5500 ms the target was flashed for 10 ms. After the end of the movement the ruler appeared and subjects had to indicate the perceived position of the target. (c) Spatial distribution of the 5 targets for all experiments.

2.5. OKN trials

In the OKN condition, the moving RDP was visible for 6000 ms. The localization target was flashed after 5500 ms. Subjects were instructed to attentively watch the display without actively pursuing any elements of the RDP.

2.6. Fixation/background motion trials

During these trials subjects fixated the central fixation point on the gray background (pure fixation), or while the RDP was presented (fixation with background motion). The timing of these trials matched that of the “free viewing” or OKN trials, respectively.

2.7. Procedure

Each experimental session consisted of 100 trials. At the end of each trial, a ruler (see above) was displayed, which could be oriented either horizontally or vertically on the screen. Subjects indicated the perceived location of the flash with respect to this ruler. Ruler orientation was kept constant within sessions.

Each subject performed 4 free viewing sessions, 4 fixation sessions without background motion, and 4 fixation sessions with background motion. Half of these sessions used a vertical ruler, the other half a horizontal ruler. Each subject also performed 6 OKN sessions (4 with horizontal and two with vertical ruler orientation). Fig. 1 shows the temporal evolution of a single trial for free viewing (a) and the OKN-condition (b).

2.8. Data analysis

For the analysis of localization errors during the slow-phase only trials in which no saccade was initiated in a time-window ranging from 100 ms before

to 100ms after the onset of the flash were considered. Localization errors were computed independently for the 5 flash locations. Trial-averaged errors in horizontal and vertical directions were combined to a resultant 2-D error vector. In a first step, we determined the errors in the free viewing condition. Then we computed the errors in the OKN condition. Net errors were computed by subtracting the error in the free viewing condition from the error during OKN.

We were also interested in the dynamics of the mislocalization around the time of a fast-phase. To this end, we computed a moving average of the perceived flash location as a function of time relative to the onset of the temporally closest fast-phase from 200 ms before onset of the fast-phase until 200 ms thereafter. These mislocalization errors were smoothed with a Gaussian shaped weighing function ($\sigma = 8$ ms). To verify that the errors were due to the subjects' eye movements and not to the background motion, we tested localization performance during fixation. Again, we determined the localization errors during fixation of a homogenous background and the localization error during fixation and simultaneous background motion. The baseline-corrected error was computed by subtracting the error in the fixation condition from the error during background motion. If not stated otherwise data are presented as means \pm SD.

3. Results

We present our results in two parts. First, we demonstrate that during the slow-phase the eye movements of the OKN bias the perception of position in the direction of the eye-movement. Second, we analyze the time course of mislocalization during OKN and show that the fast-phase eye movements modulate this mislocalization in a manner that is reminiscent of the mislocalization during voluntary saccades in darkness.

3.1. Experiment 1

To keep experimental conditions as comparable as possible in this experiment we chose to use localization during free viewing instead of e.g. localization during fixation as baseline condition. The introduction of a fixation point (and the task to precisely fixate it) would probably cause differences in attentional load between the conditions. Furthermore a fixation point could serve as a reference and thereby influence localization.

3.2. Eye movements during free viewing and OKN

Since free viewing is an unconventional condition we will briefly describe eye movements under this condition and compare them with those measured during OKN. Saccade frequency averaged across subjects was 1.73 ± 0.35 Hz during free viewing and increased to 2.79 ± 0.41 Hz during OKN. Total (2-D) saccade amplitude was quite similar under both conditions (2.46 ± 0.99 deg during free viewing and 3.12 ± 0.70 deg during OKN, respectively). While horizontal and vertical saccade components were of comparable magnitude during free viewing (horizontal: 1.80 ± 0.59 deg, vertical: 1.62 ± 0.91 deg; $p > 0.5$, Mann–Whitney Rank Sum Test) they differed significantly during OKN (horizontal: 2.97 ± 0.73 deg, vertical: 0.88 ± 0.27 deg;

$p < 0.001$, Mann–Whitney Rank Sum Test). During free viewing the average eye position (calculated from 500 ms after trial-initiation until flash presentation) was slightly above (0.29 ± 0.27 deg) and to the right (0.16 ± 0.13 deg) of the center of the screen (Figs. 2a and d; 3a). During OKN mean eye position differed significantly ($p < 0.001$, Mann–Whitney Rank Sum Test), for leftward and rightward background motion (“shift of the beating-field”). During leftward background motion the average eye position was shifted 3.46 ± 1.24 deg to the right while it was shifted 3.28 ± 1.50 deg to the left during rightward background motion. Vertical eye position was similar under both conditions (0.12 ± 0.30 deg vs. 0.03 ± 0.34 deg for leftward and rightward background motion, respectively).

3.3. Experiment 1a: localization during free viewing

Fig. 2 shows the results of the first experiment for two subjects. The upper graphs (a, d) show localization errors during free viewing. On average, each line represents data from about 70 trials for subject AK and 75 trials for subject AR. Localization was not veridical but biased towards a location below the center of the screen. The same pattern of errors was observed averaged across subjects (Fig. 3a). On average, each data line is based on about 580 trials.

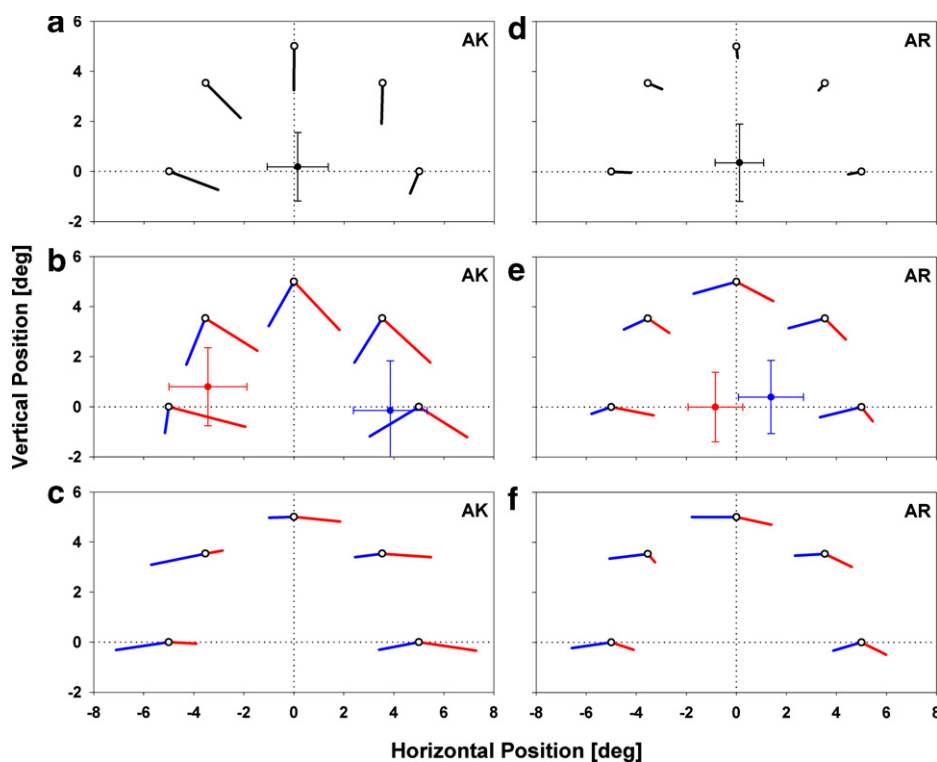


Fig. 2. Localization errors during eye movements. The graphs show the mislocalization during free viewing (a and d) and stimulus induced eye movements without (b and e) and with (c and f) baseline correction for subjects AK and AR. Black circles indicate the flash positions. Lines emanating from these circles point towards the perceived flash position (located at the end of each line). Black lines show localization errors without background motion (free viewing), blue lines show the errors for leftward and red lines for rightward background motion (OKN condition). Crosses mark the average eye position (black: free viewing, blue: leftward background motion and red: rightward background motion). The dashed lines show the horizontal and vertical meridian, respectively, which cross each other at the center of the aperture.

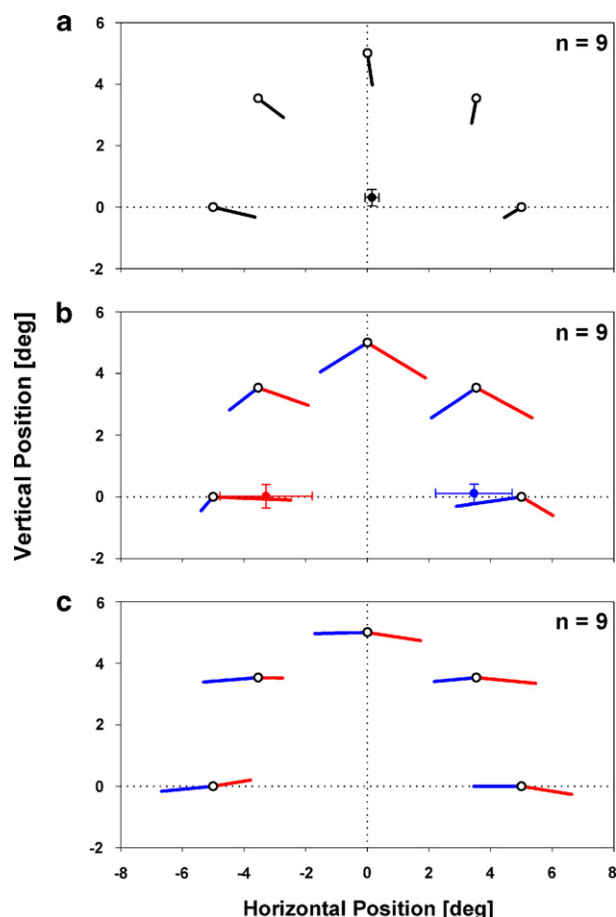


Fig. 3. Localization errors during eye movements. The graphs show the mislocalization during free viewing (a) and eye movement condition without (b) and with (c) baseline correction for the group of $n = 9$ subjects. Other conventions as in Fig. 2.

3.4. Experiment 1b: localization during OKN slow-phase

During the slow-phase of the OKN (Fig. 2b and e) we observed a mislocalization in direction of the eye movement. On average, each line represents data from about 24 trials for subject AK and 28 trials for subject AR. After correction for the bias obtained in the baseline condition (i.e. by subtracting the localization errors during free viewing measurements (Fig. 2a and d) from those during OKN slow-phase (Fig. 2b and e)), the remaining shift was clearly in the direction of the slow-phase eye movement (c and f). This perceptual effect was also observed when data were averaged across subjects (Fig. 3b and c). In this case each data line in Fig. 3b is based on about 200 trials.

To investigate the influence of the position of the flash on the localization, we analyzed horizontal (Fig. 4a) and vertical (Fig. 4b) error components independently of each other. Localization errors during OKN slow-phase are plotted as a function of horizontal flash position. The effect of motion direction on the horizontal localization error was significant for all flash positions for each individual subject as well as averaged across subjects (in all cases: $p < 0.001$, Mann–Whitney Rank Sum Test). The (horizontal) OKN,

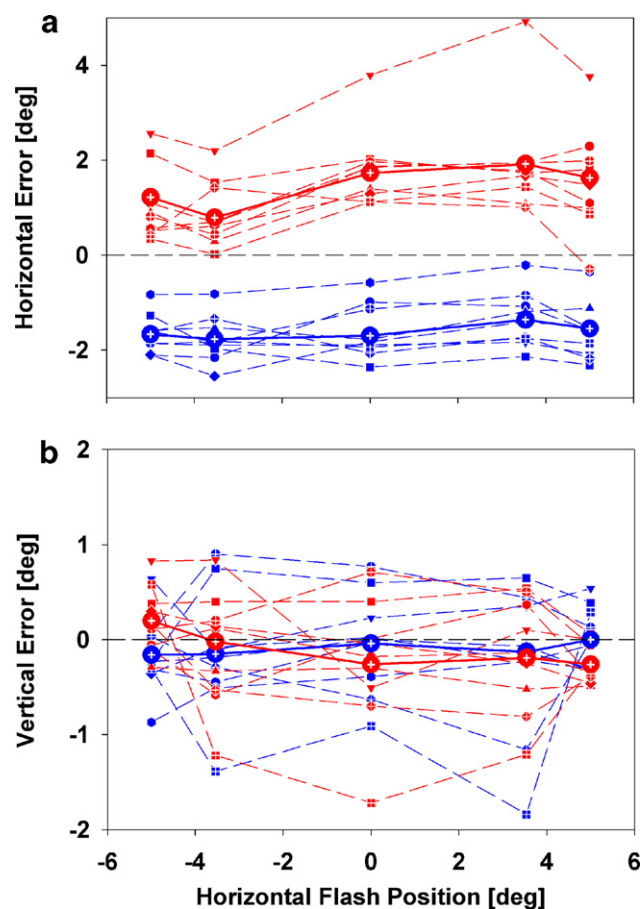


Fig. 4. Corrected horizontal (a) and vertical (b) localization errors as a function of flash position on the screen. Positive errors indicate rightward (upward) mislocalization, negative errors leftward (downward) mislocalization. Dashed curves show single subject data, solid curves show population data. Curve color indicates background motion direction (blue: leftward, red: rightward).

however, had no significant effect on vertical localization errors ($p > 0.9$, Mann–Whitney Rank Sum Test).

Moreover, statistical analysis did not reveal any significant influence of flash position, on vertical localization error ($p > 0.1$ for rightward and $p > 0.8$ for leftward motion, ANOVA on Ranks). While there was no significant influence of flash-position on the horizontal localization error for leftward motion ($p > 0.6$, ANOVA on Ranks) there was some influence for rightward motion ($p < 0.05$, ANOVA on Ranks). To test if the distance of the flash from the fovea could cause this effect we analyzed the relationship between horizontal localization error and the horizontal distance between flash and fovea at the time of the flash (Fig. 5). For leftward motion (a) we found a minimal but significant correlation between the horizontal localization error and the horizontal distance of the flash relative to the fovea ($R^2 = 0.0081$, $p < 0.02$). For rightward motion (b) the correlation was stronger though still small ($R^2 = 0.084$, $p < 0.001$). Linear regression revealed an increase of perceptual error with increasing retinal eccentricity (for fit-parameters see Fig. 5).

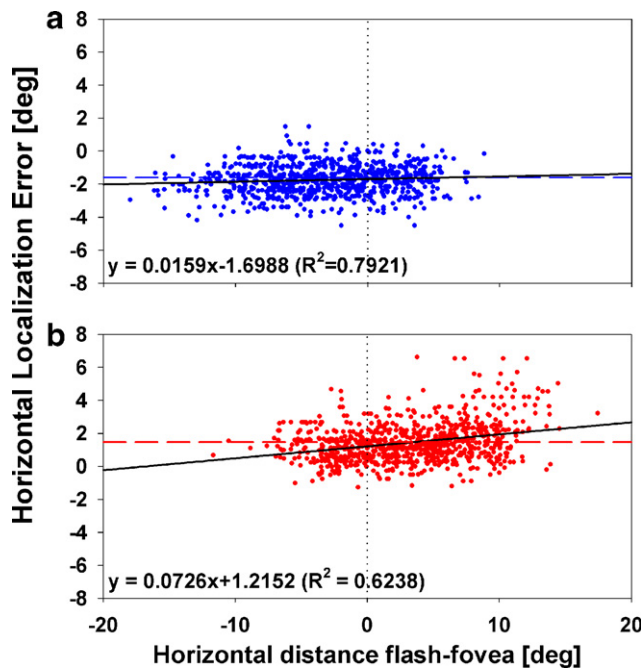


Fig. 5. Corrected horizontal localization errors as a function of stimulus position relative to the fovea for leftward (a) and rightward (b) background motion. Positive errors indicate rightward mislocalization. The dotted lines mark the position of the fovea at the time of the flash. Points to the right of the dotted line depict trials during which the target was presented to the right of the fovea. Solid lines represent linear regressions to the data while dashed horizontal lines show mean errors.

3.5. Experiment 2

In principle, the mislocalization during the slow-phase eye movements shown in Figs. 2–4 could have been caused by either the eye movements, the presence of background motion, or both. To determine the relative contributions of these sources of perceptual error we introduced a fixation point in the center of the display to suppress optokinetic eye movements while keeping the remaining stimulus conditions identical.

3.6. Experiment 2a: localization during fixation

In the absence of background motion, localization was again biased towards the center of the screen (Fig. 6a), which in this experiment is the same as the fovea. However, mislocalization was significantly larger ($p < 0.001$, Wilcoxon Signed Rank Test) than under free viewing and more uniform across subjects. Lines represent data from about 660 trials each.

3.7. Experiment 2b: localization during background motion

During background motion (Fig. 6b and c) the horizontal component of the localization error was only 17% of the error we observed during OKN. This reduction was statistically significant ($p < 0.001$, Mann–Whitney Rank Sum Test). Nevertheless, it should be noted that the effect of

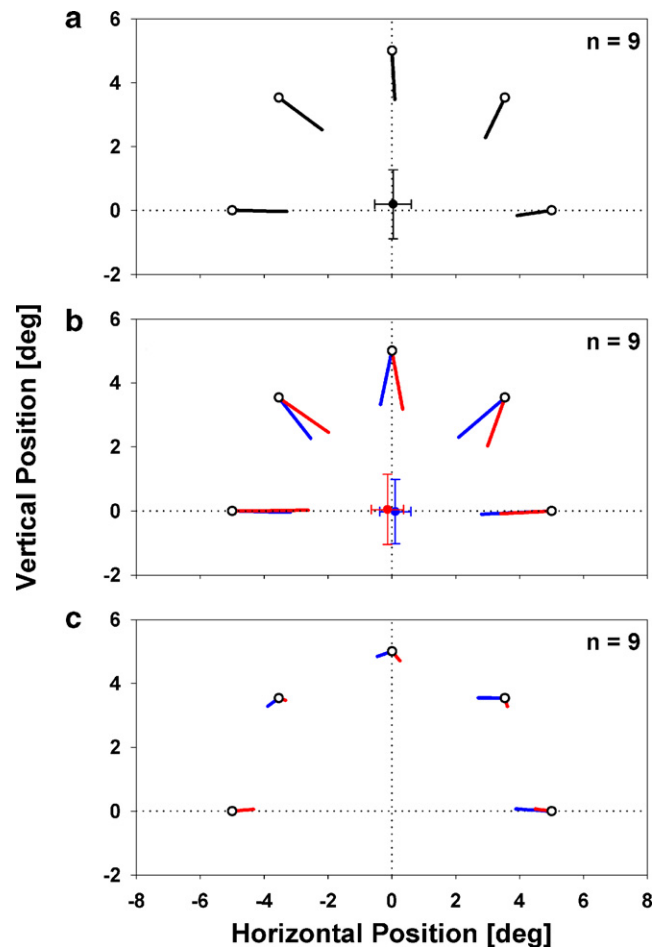


Fig. 6. Localization errors during fixation. The graphs show the mislocalization during baseline (a) and background motion condition without (b) and with (c) baseline correction for the group of $n = 9$ subjects. Other conventions as in Fig. 2.

background motion on localization (left vs. right) was significant ($p < 0.001$). In summary, background motion could account for approximately 17% of the mislocalization value during OKN. The remaining 83% of the mislocalization must therefore be attributed to the eye movements themselves. Lines in Fig. 6b represent on average data from about 310 trials each.

3.8. Dynamics of the localization error

OKN is an alternating pattern of slow-phases (in the direction of the stimulus motion) and fast-phases (opposite to the direction of stimulus motion). After showing that most of the localization error was due to the eye movements we were interested if mislocalization was different during the slow and fast-phases. We first calculated the corrected horizontal localization error as a function of time relative to the onset of the temporally closest fast-phase pooling across all flash positions and subjects. Then, we computed a moving average across these data-points independently for both motion directions (Fig. 7). Note that the overall curves are shifted away from zero. This reflects the findings shown in Figs. 2–4; the mean

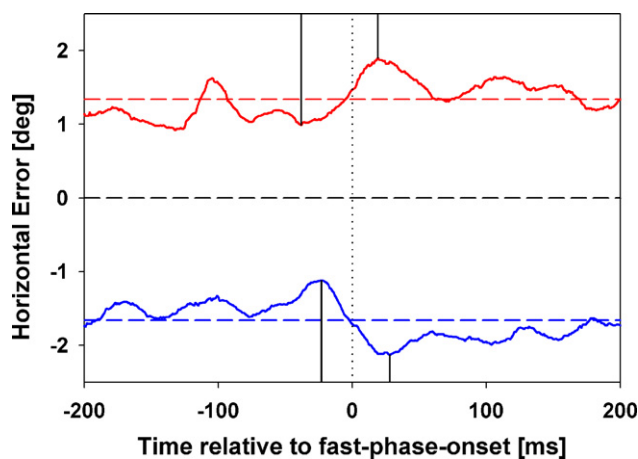


Fig. 7. Horizontal localization errors as a function of time relative to the onset of the temporally closest fast-phase. Positive errors indicate rightward mislocalization. Red and blue dashed horizontal lines represent mean localization errors. The dotted vertical line marks the onset of the fast-phase. Curves are moving averages obtained from the data with a 31 ms wide Gaussian weighted window. Red represents rightward background motion and blue leftward background motion. Solid vertical lines denote the timing of maxima and minima of the curves temporally closest to the onset of the fast-phase.

error points in the direction of the slow eye movement for both motion directions (positive values indicate errors directed to the right, negative values indicate errors to the left). Shortly before a saccade, however, the magnitude of the bias decreased. This modulation was in the direction of the fast-phase. After the fast-phase the bias in the direction of the slow eye movement temporarily increased.

The effect of the fast-phase eye movements can be described as a biphasic, additive mislocalization. This additive mislocalization lasted approximately 100ms, i.e. ± 50 ms centered on fast-phase onset. Its effect was first in the direction of the fast-phase (peaking 25ms before fast-phase onset), crossed zero at fast-phase onset, and then caused a mislocalization against the direction of the fast-phase (peaking 25ms after onset). This modulatory pattern was the same for all flash positions, i.e. we found no evidence for a perceptual compression of space during the fast-phases.

4. Discussion

We showed that reflexive eye movements cause consistent perceptual mislocalization of briefly presented visual stimuli. These mislocalizations were similar to those observed during smooth pursuit and voluntary saccadic eye movements, but there were some notable differences. This section will discuss our findings in the light of the known properties of perceptual mislocalization during voluntary eye movements.

4.1. Mislocalization during smooth pursuit and OKN slow-phase

Visual targets presented during smooth pursuit eye movements are mislocalized in the direction of pursuit

(Brenner et al., 2001; Mateeff et al., 1981; Mitrani et al., 1979). This is clearly very similar both in sign and in magnitude (Mateeff, Mitrani, & Stojanova, 1982; Mitrani & Dimitrov, 1982; Mitrani et al., 1979) to our findings. Differences become apparent when the spatial properties of the error patterns are compared. During smooth pursuit, targets flashed in the visual hemifield for which the fovea is headed are subject to strong mislocalization. Target locations in the other hemifield (i.e. where the fovea comes from) are mislocalized less markedly (Mitrani & Dimitrov, 1982; Rotman et al., 2004; van Beers et al., 2001). This was not the case during OKN. In our experiments we tested a horizontal range of target positions of 10° . Due to the spatial arrangement of the targets, not all target locations were projected into the same retinal hemifield. Depending on the length of the OKN-slow-phase and the previous shift of the beating-field, the target could be projected onto a parafoveal or more peripheral part of the retina, being either within the nasal or temporal half of the retina. Yet, different from the results during smooth pursuit, we observed substantial localization errors in both hemifields. In addition we found only minimal (leftward background motion) or minor (rightward background motion) dependencies of the localization errors on retinal eccentricity. The observed error could be interpreted as a slight overestimation of the retinal eccentricity which has also been observed during smooth pursuit (Rotman et al., 2004).

Mislocalization during pursuit is often explained by a temporal mismatch between the visual and the eye position signal (Brenner et al., 2001; Schlag & Schlag-Rey, 2002). The spatial dependence of the perceptual error during pursuit, however, suggests that this is either not the only error-component during pursuit (Mitrani & Dimitrov, 1982; Rotman et al., 2004) or that eye position signals and retinal signals are matched differently for different parts of the visual field (van Beers et al., 2001). Since misperception during OKN slow-phase was (predominantly) independent of target position in our experiments our results could be explained simply by the combination of an erroneous eye position signal with the visual signal.

The neural systems underlying OKN and smooth pursuit have been well studied. Early studies emphasized the differences between these systems (Carpenter, 1988) and as such one might expect a difference in localization during OKN and pursuit. More recent studies, however, have revealed a much tighter link. For instance, a lesion of the most important subcortical structure for the control of the OKN, the Nucleus of the Optic Tract (NOT-DTN), also affected pursuit performance (Ilg, Bremmer, & Hoffmann, 1993). Moreover, imaging studies showed that the same cortical networks were active during smooth pursuit and OKN (Konen et al., 2005). In this context, our finding that localization during OKN does not depend on target position while localization during smooth pursuit does, is somewhat surprising. As we will discuss below in the context of fast-phase OKN, one important factor may be the absence of an explicit visual target during OKN.

4.2. Mislocalization during saccades and OKN fast-phase

A number of studies have shown mislocalization of briefly presented visual targets during visually guided saccades (for review see: Ross, Morrone, Goldberg, & Burr, 2001; Schlag & Schlag-Rey, 2002). The exact pattern of perisaccadic spatial distortion heavily depends on the exact environmental conditions. A unitary shift of perceived stimulus locations is observed in total darkness (Cai et al., 1997; Lappe et al., 2000). In the presence of visual references, however, the same spatial arrangement of target positions leads to a perceptual compression of space (Ross et al., 1997).

In our experiments the error pattern observed during fast-phase OKN was independent of position. Moreover, the modulation of perceived position by the fast-phases revealed a biphasic pattern that has also been observed for visually guided saccades in total darkness (Honda, 1989). Yet, the time course of the observed effects was different in the two cases: during visually guided saccades, the peak mislocalization in the direction of the saccade occurred at saccade onset, while for OKN fast phases the peak mislocalization was observed about 25 ms prior to fast-phase onset. Taken together the error pattern we observed is somewhat similar to the perisaccadic shift even though the stimulus conditions led us to expect a compression of space.

The prime candidate mechanism for perisaccadic shifts is a mismatch between the actual eye position and a sluggish or damped neural eye position signal (Dassonville et al., 1992; Honda, 1991). Given the spatial similarity in the perceptual effects, this mechanism could underlie mislocalization during fast-phase OKN as well. The different time courses of the effects during OKN and visually guided saccades might be indicative of different lengths of neural processing being necessary in the one or the other case. The question, however, arises why the mechanism that causes saccadic compression does not seem to be active during OKN. One explanation could be that – unlike during voluntary saccades – there is no clearly defined target position for the fast phase eye movement. In the two-step model of perisaccadic localization (Awater & Lappe, 2006) such uncertainty about the position of the eye abolishes the compression. At the neural level, perceptual stability and perisaccadic localization are far from understood, but a number of studies have shown that receptive field properties change before voluntary saccades in many visual areas (LIP: Duhamel, Colby, & Goldberg, 1992, V3–V1: Nakamura & Colby, 2002, V4: Tolias et al., 2001, MT/MST: Krekelberg, Kubischik, Hoffmann, & Bremmer, 2003). Recently, we have shown that such RF shifts in MT can also be observed during OKN (Hartmann, Bremmer, Albright, & Krekelberg, 2006).

Our data also show an enhanced perceptual error in the direction of the slow eye movement briefly after the fast-phase. This effect is reminiscent of the increased sensitivity to optokinetic stimulation briefly after a voluntary saccade (Kawano & Miles, 1986), which has recently been linked to

an enhanced postsaccadic neural response in area MT (Ibbotson, Price, Crowder, Ono, & Mustari, 2006). It is, however, also possible that the large retinal slip that occurs during this period affects the mislocalization in a purely visual manner (as the background motion did in experiment 2b).

4.3. Mislocalization during fixation and free viewing

Localization during fixation was not veridical. Perceived flash positions during free viewing were shifted towards a point below the center of the display, while subjects on average looked at a point slightly above and to the right of the center of the display. This is in contrast to previous experiments which reported mislocalization towards the point of fixation (van der Heijden, van der Geest, de Leeuw, Krikke, & Musseler, 1999). During active fixation, perception was shifted towards the fixation point. Interestingly, the mislocalization was stronger than during free viewing. One explanation could be that the eye position of the subjects at the time of the flash was less consistent in the free viewing condition ($x: 0.51 \pm 1.44$ deg, $y: 0.7 \pm 1.85$ deg; averaged across all trials) than in the fixation condition ($x: 0.07 \pm 0.73$ deg, $y: 0.23 \pm 1.30$ deg). Although speculative, another explanation might be based on differential receptive field (RF) properties of cortical neurons during free viewing and active fixation. When a macaque monkey freely views a homogeneous gray monitor, LIP RFs have a smaller maximum response and a more peripheral center of gravity than during active fixation (Ben Hamed, Duhamel, Bremmer, & Graf, 2002). In other words, active fixation shifts the average LIP RF toward the straight ahead position. Currently, it is not clear whether such RF changes also occur in the putative human homologue of macaque area LIP (Konen et al., 2004). Recently an influence of attention on the position of RFs in macaque area MT has been demonstrated (Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). In about two thirds of the cells the center of mass of the RFs is shifted in direction of the focus of attention. Similar results have been observed in area V4 (Connor, Preddie, Gallant, & van Essen, 1997). Though we did not explicitly vary attention in our experiment these results are interesting with regard to our study since they suggest that active/attentive fixation of a visual stimulus (here: the fixation point) may have shifted visual receptive fields.

5. Conclusion

In summary, we showed that briefly flashed visual targets are mislocalized during reflexive eye movements. This mislocalization is similar to that observed during voluntary eye movements in darkness and did not show the typical spatial variation observed when voluntary eye movements are performed in the presence of visual references. In other words, the localization mechanisms operating during reflexive eye movements appear not to use visual references even though some are available. We speculate that the reason for

this may be that the strongest of visual references – the visual target of an eye-movement – is absent during reflexive eye movements. One could even say that these reflexive eye movements have no (conscious) target at all. This interpretation provides further confirmation of the importance of the eye movement target, as a reference, in the linking of pre- and postsaccadic coordinate systems (Awater & Lappe, 2006; Deubel, 2004; Deubel, Bridgeman, & Schneider, 1998). This work was supported by the DFG (Research Group 560 “Perception and Action” and Research-Training-Group-885 “NeuroAct”).

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