

# Perisaccadic Mislocalization Orthogonal to Saccade Direction

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## Summary

**Saccadic eye movements transiently distort perceptual space. Visual objects flashed shortly before or during a saccade are mislocalized along the saccade direction, resembling a compression of space around the saccade target. These mislocalizations reflect transient errors of processes that construct spatial stability across eye movements. They may arise from errors of reference signals associated with saccade direction and amplitude or from visual or visuomotor remapping processes focused on the saccade target's position. The second case would predict apparent position shifts toward the target also in directions orthogonal to the saccade. We report that such orthogonal mislocalization indeed occurs. Surprisingly, however, the orthogonal mislocalization is restricted to only part of the visual field. This part comprises distant positions in saccade direction but does not depend on the target's position. Our findings can be explained by a combination of directional and positional reference signals that varies in time course across the visual field.**

## Introduction

Saccades are quick, goal-directed eye movements that subserve accurate high-resolution foveal vision. During saccades, the projection of the world sweeps across the retina at high speed, but this visual motion is not perceived. Despite the difference in the retinal picture before and after saccades, the world continues to appear visually stable. Von Helmholtz (1866) thought that visual stability is preserved because the motor command related to the desired eye movement is used by the visual system to predict changes to the visual input. Such an internal feedback signal, named corollary discharge (Sperry, 1950) or efference copy (von Holst and Mittelstaedt, 1950), could compensate for the shift of the retinal image. In addition, visual comparisons between pre- and postsaccadic images or visual motion cues during the saccade could also be used to establish perceptual stability (Deubel et al., 1998; Niemeier et al., 2003).

Whereas under normal conditions perceptual stability is preserved during saccades, the perception of the position of objects flashed shortly before or during a saccade is altered (Ross et al., 2001; Schlag and Schlag-Rey, 2002). An object flashed during a saccade is perceived at an illusory position, and the magnitude of this mislocalization depends on the object's position in the visual field (Mach, 1885; Matin and Pearce, 1965). During horizontal as well as vertical saccades performed in a dark environment, a shift of apparent position in the direction of the saccade can be observed (Honda, 1989, 1991; Schlag and Schlag-Rey, 1995). This effect even occurs for objects flashed *before* the start of the saccade (Honda, 1995; Cai et al., 1997). With background illumination or visual references available, objects presented beyond the target position are shifted backward along saccade direction toward the target (Ross et al., 1997; Morrone et al., 1997; Lappe et al., 2000). These short-term perceptual errors are believed to be related to the processes that subserve transsaccadic perceptual stability of vision.

A model of these observed mislocalizations was based on the retinal eccentricity of the mapping of the flashed object on the retina (Morrone et al., 1997). The calculation of the perceived position involved three components: the shift of the coordinate system caused by the saccade, the compression of the metric of space during saccades, and the eye position at object presentation time. While the shift component in this model could correspond to an efference copy signal, the origin of the compression component is less obvious. A contribution of visual factors is likely, because the compression component is strongest when visual reference objects are present at saccade offset (Lappe et al., 2000).

Several brain structures have been hypothetically linked to effects of perisaccadic mislocalization. As mislocalization occurred for objects presented before the saccade, regions active before saccade onset are possible candidates. In the superior colliculus (SC), for example, neurons are active about 40 ms after target presentation and 200 ms before the start of a saccade (Walker et al., 1995). In the frontal eye field (FEF), 20% of the neurons are active within 60 ms after target presentation, and a broad activity starts 100 ms before the saccade (Umeno and Goldberg, 1997). In the intermediate layers of SC, in FEF and in LIP (lateral intraparietal area) a shift of the receptive field (remapping) occurs around the time of saccades (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997). In LIP, receptive fields of some neurons shift even before saccade initiation (Duhamel et al., 1992; Colby et al., 1995), suggesting that this area could be involved in a presaccadic updating of visual spatial representations. Tolia et al. (2001) reported that receptive fields of neurons in area V4 shift and shrink before a saccade. The shift of the receptive field centers in these neurons is not along the saccade direction, i.e., not only in horizontal direction for horizontal saccades, but rather directed toward the saccade target, i.e., receptive fields shifts toward the target have components orthogonal to saccade direction. Tolia et

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al. (2001) suggest that the receptive field shifts result from attentional effects associated with the preparation of a saccade. Neurons in the middle temporal (MT) and medial superior temporal (MST) areas of the primate dorsal stream change their response properties to moving or flashing visual stimuli during saccades (Thiele et al., 2002). When evaluated in a population code, their responses predict perisaccadic localization errors similar to spatial compression (Krekelberg et al., 2003).

To understand the origin of perisaccadic mislocalization it is important to know whether perceptual position shifts are coaligned with saccade direction or whether mislocalizations occur also in directions orthogonal to the saccade. Different proposed mechanisms for perceptual stability would predict different types of perisaccadic localization errors. A first class of mechanisms uses reference signals for the amplitude of the eye movement, such as an efference copy of the eye movement or the visual motion experienced during the saccade. These mechanisms would predict mislocalization only along the direction of the saccade. For instance, Honda (1991) suggests that the reference signal first overestimates eye position and at later times underestimates eye position, giving rise to mislocalizations first in and later against saccade direction. Because horizontal and vertical eye movements are generated by different brain stem structures, efference copy signals may be different for horizontal and vertical saccades. In each case, however, errors should be coaligned with eye movement direction, and Honda (1989, 1991) found no difference in time course or magnitude of errors for horizontal and vertical saccades.

A second class of mechanisms uses positional reference signals such as visual, attentional, or reafferent references of the saccade target, a transient foveal bias of localization, or representational errors in neuronal populations. These mechanisms should predict mislocalization also in two dimensions. Previous studies reported shift toward the target only along saccade direction and not orthogonal to it (Honda, 1993; Morrone et al., 1997). For a horizontal saccade, a flashed object would be perceived horizontally near the target position but not shifted along the vertical axis. However, in the experiments described below we show that orthogonal mislocalization does occur, although unexpectedly only for part of the visual field. Furthermore, we discuss why the effect has not been found previously and what could be possible reasons for its occurrence.

## Results

We asked three observers to locate a briefly flashed (12 ms) green dot on a red background on a computer monitor in a dimly lit room while they were making rightward saccades of 20° amplitude. The dot was flashed at variable times before or after saccade onset (see Figure 1 and Experimental Procedures). It appeared randomly at one of a set of different locations around the saccade goal. Subjects reported the perceived location of the flashed dot with a mouse pointer after each trial. A ruler on the screen provided visual references at all times. It consisted of a black horizontal line with vertical tick marks at -20°, -10°, 0°, 10°, and 20°. Fixa-

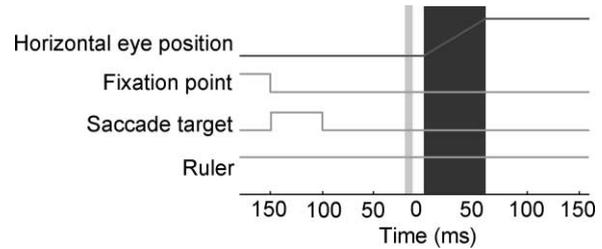


Figure 1. Timing of Events in a Single Trial

The trial started with the presentation of a fixation point for 500–1500 ms. When the fixation point disappeared and the saccade target was shown for 50 ms, the subject made a saccade with a certain latency. The dark gray bar represents the onset and duration of the saccade. Some time before, during, or after the saccade, a green dot (luminance 43 cd m<sup>-2</sup>; diameter 1.2°) was flashed for one video frame (12 ms). The light gray bar indicates the time and duration of the flash dot in the case when it was presented just before saccade onset. The position of the dot was chosen pseudorandomly from a grid of possible positions. Subjects were asked to report the perceived position of the dot with a mouse pointer that became visible 500 ms after the flash.

tion point and saccade target positions were indicated on the ruler by tick marks. In later experiments with 12°, 16°, and 24° saccade amplitudes, an additional tick mark was added at the respective saccade target position.

Apparent horizontal and vertical position of the flashed dot was recorded as a function of the presentation time of the dot relative to the onset of the saccade and the true position of the dot. Each data point in Figure 2 is a single trial measurement. Data from different subjects can be distinguished by color. Figures 2A and 2B show a clear, time-dependent mislocalization toward the saccade target along the horizontal direction, similar to results of previous studies (Ross et al., 1997; Lappe et al., 2000). This mislocalization begins 50 ms before saccade onset and peaks when the saccade starts. In addition, there is also a strong mislocalization toward the saccade target in the vertical direction (Figures 2C and 2D). This mislocalization is orthogonal to the direction of the saccade. Therefore, it cannot be explained by a directional reference signal associated with the saccade.

Orthogonal mislocalization occurred only in part of the visual field. We systematically mapped the mislocalization in the area around the saccade target as shown in Figure 3. For each trial, the presented dot was randomly chosen from one of 24 positions that formed a grid around the saccade target (Figure 3A). As the three subjects showed similar time courses and magnitudes of mislocalization (see statistical analysis below and compare Figure 2), their data were collapsed. Figure 3B shows for the pooled data the pattern of mislocalization for the possible dot positions. The arrowhead points to the median apparent position in the time interval of 10 ± 7 ms after saccade onset, when the effects were generally largest. The arrow tail is the baseline position calculated from trials in which the dot was presented more than 90 ms before or more than 70 ms after the beginning of the saccade, i.e., when the perisaccadic effects were not present (note that in this and subsequent experiments the baseline shift in the upper visual field was

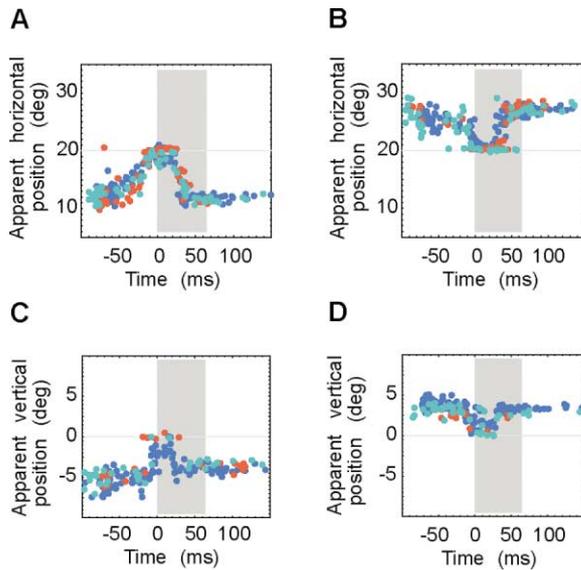


Figure 2. Examples of Time-Dependent Mislocalization for Horizontal 20° Saccades for the Three Subjects

HF, blue; HA, red; ML, cyan. Each point is the reported dot position in one single trial. The vertical gray line indicates the time of the saccade. The horizontal gray line indicates the saccade target's position. (A) Horizontal mislocalization toward the target for dots presented at position (12°, -4°). (B) Horizontal backward mislocalization toward the target (i.e., against saccade direction) for dots presented at position (28°, 0°). (C) Vertical upward mislocalization (i.e., orthogonal to saccade direction) for dots presented at position (28°, -4°). (D) Vertical downward mislocalization (i.e., orthogonal to saccade direction) for dots presented at position (28°, 4°).

slightly larger than in the lower visual field, similar to previous findings on peripheral localization during fixation [Osaka, 1977].

During the saccade, apparent positions are shifted

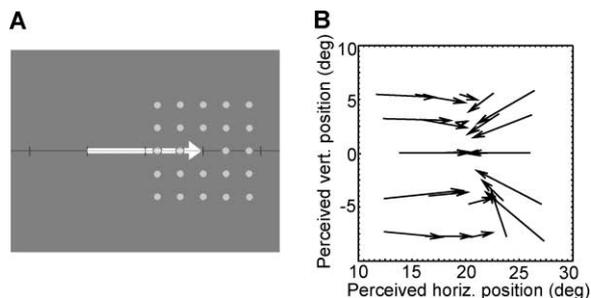


Figure 3. Spatial Pattern of Mislocalizations for a 20° Horizontal Saccade

(A) Saccade metric and dot positions for a horizontal 20° saccade. The arrow indicates the eye trajectory from fixation point to saccade target. The dots show the possible positions of the flashed dot. (B) Spatial pattern of mislocalization during the saccade. Each arrow indicates the mislocalization for one dot position. The arrow points from the baseline perceived position, i.e., the median perceived position for dots presented more than 90 ms before or 70 ms after saccade onset, to the median perceived position in the interval of  $10 \pm 7$  ms after saccade onset (peak mislocalization). The figure contains collapsed data from all three subjects. Vertical components of mislocalization toward the target occur only for dot positions on the right.

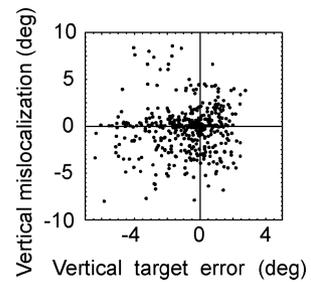


Figure 4. Vertical Mislocalization versus Vertical Target Error  
Comparison of saccade landing error (inadvertent vertical component of the saccade direction) and vertical component of mislocalization for trials in which the dot was flashed during peak mislocalization time (5–25 ms after saccade onset). There is no correlation between landing position and perceived object position ( $r = 0.027$ ). Thus, vertical components of mislocalization do not arise from inadvertent vertical components of the eye movement.

horizontally toward the saccade target. In addition, points on the right side of the target are also shifted vertically, revealing mislocalization orthogonal to saccade direction in the space beyond the saccade target. We tested the observed orthogonal mislocalization for statistical significance for the three subjects individually. For all positions, the perceived vertical positions for baseline (more than 90 ms before or 70 ms after saccade onset) were compared to the perceived positions during peak mislocalization (5–25 ms after saccade onset) using a t test as implemented in Mathematica. Significant vertical shift ( $p < 0.05$ ) occurred at positions (24°, 8°), (28°, -8°), (28°, -4°), (28°, 4°), and (28°, 8°) for subject HF, at positions (24°, -8°) and (24°, 8°) for subject HA, and at positions (24°, -4°), (24°, 8°), and (28°, 4°) for subject ML.

The occurrence of vertical mislocalization in perception did not result from inadvertent vertical components of the eye movement. We compared the perceived position during the peak time of mislocalization (5–25 ms after saccade onset) with the deviation of the landing point of the saccade from the saccade target (Figure 4; note that for this analysis we included also trials in which the saccade was inaccurate whereas in all other data analysis trials were excluded when the landing point of the eye deviated more than 2° from the target position). There was no correlation between the mislocalization of the dot position and the saccade landing point neither along horizontal ( $r = 0.062$ ) nor vertical ( $r = 0.027$ ) direction. Proximity to the right edge of the monitor was also not the cause of vertical mislocalization at positions right of the target. In a control experiment in which fixation point, saccade target, and dot positions were repositioned leftward on the screen, orthogonal mislocalization occurred in the same area relative to the target position, even though all positions were now further away from the monitor border.

### 20° Vertical Saccade

The observation that vertical mislocalization occurred only for points to the right of the saccade target could suggest that the differences were related to remapping processes across the hemispheric border. At lower lev-

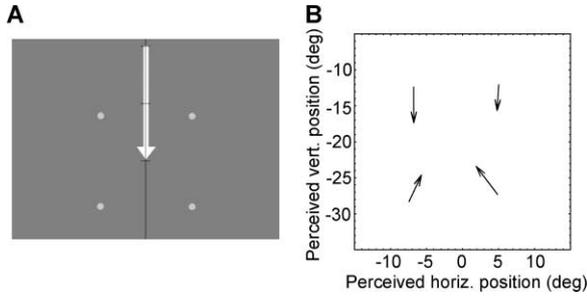


Figure 5. Saccade Metric and Dot Positions for a Vertical 20° Saccade Downward

(A) The arrow indicates the eye trajectory from fixation point to saccade target. The dots show possible positions for the flashed dot.

(B) Spatial pattern of mislocalization during the saccade. Each arrow indicates the mislocalization for one dot position. The arrow points from the baseline perceived position, i.e., the median perceived position for dots presented more than 90 ms before or 70 ms after the saccade start, to the median perceived position in the interval of  $12 \pm 7$  ms after saccade onset (peak mislocalization). The figure contains collapsed data from all three subjects. Horizontal components of mislocalization toward the target, i.e., orthogonal to the saccade direction, occur only for dot positions below the target, i.e., more than 20° away from the fixation point.

els of the visual hierarchy, one visual hemifield is mapped into one cortical hemisphere with only a small part being mapped to the other hemisphere. Objects flashed to the right of the target remain in the right visual hemifield both before and after the saccade. Dots flashed between fixation point and target position, on the other hand, fall in the right hemifield before the saccade and in the left hemifield after the saccade. In this case, the internal representation of a presaccadically presented object postsaccadically has to shift to the other hemifield, i.e., the information has to be transferred to the other cortical hemisphere. Such hemispheric transfer has recently been used to demonstrate spatial remapping during saccades in human parietal cortex (Medendorp et al., 2003; Merriam et al., 2003).

A difference between transhemispheric remapping and intrahemispheric remapping could account for the orthogonal component being present only right to the target. Alternatively, orthogonal mislocalization could simply be restricted to parts of space that lie beyond the target position in direction of the eye movement. In order to decide between these hypotheses, we measured perceived mislocalization for vertical 20° downward saccades. Four positions around the saccade target were examined (Figure 5A). The positions beyond the saccade target were now below the target position at the vertical coordinate of  $-8^\circ$ . As shown in Figure 5B, vertical mislocalization, i.e., mislocalization along saccade direction, occurred at all positions. Orthogonal mislocalization, now along the horizontal axis, occurred for positions below the target position. Hence, positions beyond the target in both visual hemifields showed orthogonal mislocalization.

We tested the observed orthogonal mislocalization for positions below the saccade target for statistical significance for all three subjects. For all positions, the perceived vertical positions for baseline (more than 90

ms before or 70 ms after saccade onset) were compared to the perceived positions during peak mislocalization (5–25 ms after saccade onset) using a t test as implemented in Mathematica. Horizontal (i.e., orthogonal) shift components toward the target were significant ( $p < 0.05$ ) for both positions below the target in subjects HF and ML and for position ( $8^\circ, -8^\circ$ ) in subject HA.

As orthogonal mislocalization was visible although no transhemispheric remapping was needed (the dot positions where in the same hemifield before and after the saccade), the first hypothesis can be excluded.

### Horizontal Saccades of Different Amplitude

In the previous experiments, orthogonal mislocalization again occurred only for dot positions spatially beyond the saccade target. Is the border of the area in which orthogonal mislocalization is expressed defined by the location of the saccade target? To investigate this question we examined mislocalization for different saccade amplitudes ( $24^\circ, 16^\circ$ , and  $12^\circ$ ). Horizontal saccades in all cases started from the same fixation point as for 20° amplitude but ended at different positions of the grid (Figures 6A, 6C, and 6E). Dots were presented on the same grid as in the case of the 20° saccades but sparing the respective position of the saccade target in each case.

For saccades with  $24^\circ$  amplitude, Figure 6B shows that mislocalization is now toward position  $24^\circ$ , i.e., the new saccade target's position. Dots presented at horizontal positions between  $12^\circ$  and  $20^\circ$  show a largely uniform shift in saccade direction up to the saccade target's horizontal position. Vertical components of mislocalization toward the target are strongly expressed for positions beyond the saccade target but also for positions above and below the saccade target. All subjects showed significant orthogonal shifts for horizontal position with more than 20° distance from the fixation point (test as in experiment I). Significant vertical shift ( $p < 0.05$ ) occurred at positions ( $24^\circ, 8^\circ$ ), ( $28^\circ, -8^\circ$ ), ( $28^\circ, -4^\circ$ ), and ( $28^\circ, 4^\circ$ ) for HF, at positions ( $24^\circ, -4^\circ$ ), ( $24^\circ, 4^\circ$ ), ( $24^\circ, 8^\circ$ ), ( $28^\circ, 4^\circ$ ), and ( $28^\circ, 8^\circ$ ) for HA, and at positions ( $24^\circ, -4^\circ$ ), ( $24^\circ, 4^\circ$ ), ( $24^\circ, 8^\circ$ ), ( $28^\circ, -4^\circ$ ), and ( $28^\circ, 8^\circ$ ) for ML. In comparison, for the 20° saccade, dot position above and below the target did not show orthogonal mislocalization (Figure 3). Therefore, it seems that the border of the area of orthogonal mislocalization was not determined by the position of the saccade target but rather by the distance of the presented dot from the initial fixation point. For both saccade amplitudes, vertical mislocalization occurred for horizontal dot positions of  $24^\circ$  and  $28^\circ$ .

In order to confirm that the area of vertical mislocalization is constrained by the distance from the fixation point rather than the location of the saccade target, we conducted two further experiments with horizontal saccades of  $16^\circ$  and  $12^\circ$  amplitude in two subjects (HF, ML). For  $16^\circ$  amplitude (Figure 6D), vertical mislocalization occurred at horizontal positions  $28^\circ$  and partly at  $24^\circ$  but not at  $20^\circ$  right next to the saccade target nor at  $16^\circ$  above or below the target. Vertical mislocalizations were significant (test as in the earlier conditions,  $p < 0.05$ ) at positions ( $24^\circ, 8^\circ$ ), ( $28^\circ, -8^\circ$ ), ( $28^\circ, -4^\circ$ ), ( $28^\circ, 4^\circ$ ), and ( $28^\circ, 8^\circ$ ) for subject HF and positions ( $24^\circ, -8^\circ$ ), and

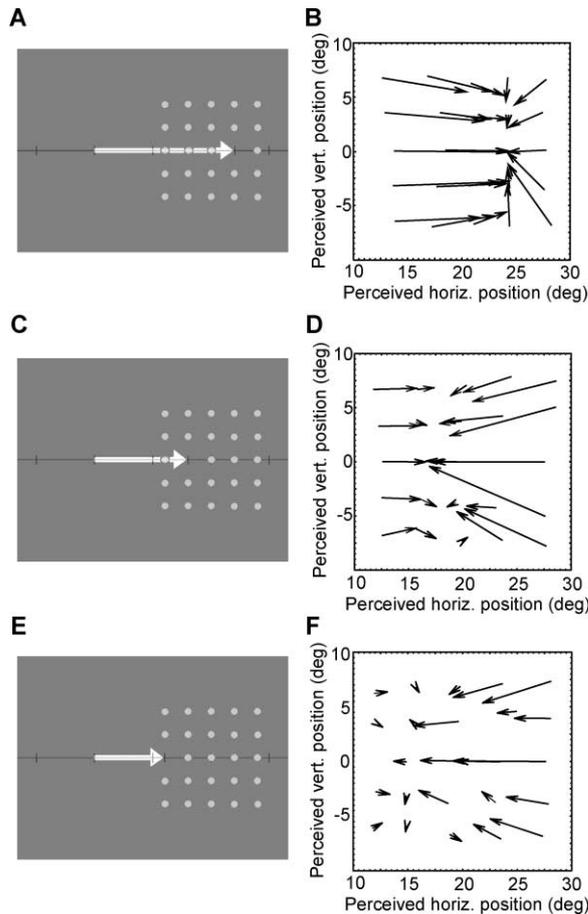


Figure 6. Spatial Pattern of Mislocalizations for 24°, 16°, and 12° Saccades

- (A) Saccade metric and dot positions for a horizontal 24° saccade. The arrow indicates the eye trajectory from fixation point to saccade target. The dots show the possible positions of the flashed dot.
- (B) Spatial pattern of mislocalization. The arrows point from the baseline perceived position before and after the saccade to the median perceived position in the interval of  $16 \pm 7$  ms after saccade onset.
- (C) Saccade metric and dot positions for a 16° saccade.
- (D) Spatial pattern of mislocalization ( $10 \pm 7$  ms after saccade onset).
- (E) Saccade metric and dot positions for a 12° saccade.
- (F) Spatial pattern of mislocalization ( $8 \pm 7$  ms after saccade onset).

(24°, -4°) for ML. Similarly, for 12° saccades (Figure 6F), positions next to the target at 12°, 16°, and 20° showed no vertical mislocalization whereas positions at higher distances from the fixation point showed vertical components [significant at positions (28°, -8°) and (28°, 4°) for HF and positions (24°, -8°) and (24°, -4°) for ML]. In all cases, however, horizontal components of the mislocalization were directed toward the horizontal position of the saccade target.

Figure 7 gives an overview of the effects of horizontal position and saccade amplitude on the magnitude of the vertical mislocalization. It shows absolute vertical mislocalization toward the target against the horizontal dot position for the different amplitudes. The vertical mislocalization was calculated as the average mislocalization (difference of perceived position from baseline) toward the target of the four dots above and below the

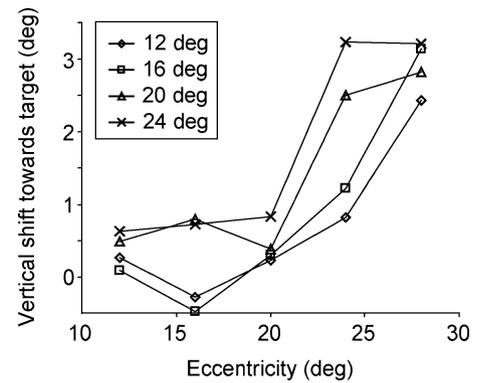


Figure 7. Dependence of Vertical Shift on Eccentricity and Saccade Amplitude

The plot gives an overview of vertical mislocalization magnitude for different saccade amplitudes (12°, 16°, 20°, and 24°) at their respective peak times of mislocalization (8–16 ms after saccade onset). The horizontal position of the flashed dots is represented as their eccentricity relative to the fixation point. The vertical mislocalization toward the target is the average mislocalization for all vertical positions at the respective eccentricity, except for dots presented on the vertical target coordinate.

ruler at the respective horizontal position. Dots positioned on the ruler, i.e., which had the same vertical coordinate as the target, were excluded. The figure shows that vertical mislocalizations of large magnitude were confined to dots at positions of 24° and 28°. If vertical mislocalization would occur beyond the saccade target, positions at 20° should show larger effects for 12° and 16° saccade amplitude than for 20° and 24° amplitude. This was not the case. The strength of vertical mislocalization, however, increased with saccade amplitude. For instance, for amplitudes of 20° and 24°, the mislocalization at eccentricity of 24° was higher than for amplitudes of 12° and 16°.

## Discussion

We conclude that dots presented far distant from the fixation point are perceptually mislocalized orthogonal to saccade direction. This type of mislocalization is inconsistent with errors in directional reference signals generated by the saccade. It suggests that positional reference signals such as the saccade target, the direction of gaze, or the orientation of the fovea are involved in perisaccadic localization. Previous studies may have missed the orthogonal component of mislocalization because their stimulus positions did not extend far enough into the periphery (Honda, 1993) or because they could not analyze the spatial distribution of mislocalization with sufficient resolution (Morrone et al., 1997).

Our results further show that the compression pattern of perisaccadic localization is not symmetric around the target. For positions close to the fixation point, the mislocalization is into saccade direction and resembles a uniform shift. At more distant positions, the mislocalization pattern is directed toward the target position in 2D and contains components orthogonal to saccade direction.

Previous models have assumed that perisaccadic

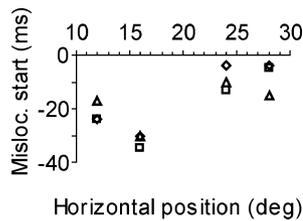


Figure 8. Timing of Perisaccadic Mislocalization Effects

Average onset time of mislocalization effects for different horizontal positions during 20° saccade (subjects:  $\diamond$  HF;  $\square$  ML;  $\triangle$  HA). The start of mislocalization was determined as the time relative to saccade onset when mislocalization was half-maximal. For positions further away from the fixation point mislocalization starts later.

mislocalization results from the combination of two processes: a shift of the reference point and a compression of distance to the reference point (Ross et al., 1997; Morrone et al., 1997). The reference point is the origin of an internal coordinate system, which shifts from the fixation point to the target during the saccade. These two processes acting differently in different parts of the visual field might explain our data.

Alternatively, temporal differences between these two processes might also lead to the observed pattern of mislocalization. As explained below, a difference in the time course between shift and mislocalization with the shift acting slightly earlier than the compression may cause mislocalization errors to depend on position in the visual field. This possibility is supported by the observation that the time at which positional errors begin to appear with respect to saccade onset varies across the visual field. We determined the beginning of mislocalization for each flash position by the point in time at which the mislocalization was half-maximal. Values for each of four horizontal positions during a 20° saccade are shown in Figure 8. Mislocalization starts earlier for positions left of the target than for positions to the right of the target. On average, mislocalization for the leftmost position was half-maximal  $23 \pm 6$  ms before saccade onset and for the rightmost position  $9 \pm 2$  ms before the saccade. The times of half-maximal mislocalization for the 24° saccade followed a similar pattern. The orthogonal displacement along the vertical axis was half-maximal on average 5 ms before the saccade for the 20° amplitude and 2 ms before the saccade for 24° amplitude. For the vertical saccade, mislocalizations started earlier for positions above the saccade target than for positions below the target.

A hypothetical model based on timing differences would be the following. The model assumes a position-dependent time course of remapping in a neuronal map of activity that represents visual events in spatial coordinates. During fixation, activity at one point of the map would encode an object at a certain external spatial coordinate. The map is assumed to be retinotopic, i.e., representing object positions in the visual field. Around the time of occurrence of the saccade, the distribution of activity is remapped to correspond to the spatial positions after the saccade. During this process the activity encoding a specific object position becomes incoherent as some neurons encode the old position

whereas others already encode the new—remapped—position, thereby smearing out the activity across the population. On its own, this effect could produce a shift of perceived position in saccade direction. A reafferent signal of the saccade target which induces activity at the target position in the map could interfere with the process of remapping. The superposition of the smeared out activity encoding the object position and the activity caused by the reafferent signal could lead to an activity peak at a position between veridical and target position. If subsequent areas estimate the position of the flashed object by the peak of activity in the map, this position would be perceived closer to the target position. In this model, whether or not an orthogonal mislocalization toward the target occurs depends on the timing between the remapping and the reafference. As suggested by our timing results, remapping starts early for positions close to the fixation point (less than 20° eccentricity) and later at further distant positions. The model assumes that when the reafferent signal arrives, positions close to the fixation point have already finished the remapping process and had exhibited only a shift in saccade direction. In contrast, positions further from the fixation point begin to enter the process of remapping at that time and would be maximally affected by the reafferent signal leading to a compression toward the target also along the orthogonal axis. This model would predict that multiple dots, presented simultaneously at eccentric positions, could be superimposed with activity caused by the reafferent signal and yield multiple activity peaks in the position map that are shifted also orthogonally toward the target. For even more eccentric positions, no orthogonal shift should be found if the reafferent signal decays before the onset of remapping at these positions. However, objects that are continuously visible should not be influenced by the reafferent signal, as their input to the map is enduring and their representation therefore stronger than that of a briefly flashed object.

A possible reason for high activity at the target position could be reafferent activity associated with saccade occurrence. The reafferent signal encoding target position could, for example, come from the superior colliculus (SC) (Sommer and Wurtz, 2002) or frontal eye field (FEF) (Hamker, 2003). A reafference from the SC could also explain why orthogonal mislocalization appears to be stronger for higher saccade amplitude. Whereas the sum of the firing rates of burst neurons in the SC remains the same for different saccade amplitudes, the sum of the firing rates of the buildup neurons increases with saccade amplitude (Anderson et al., 1998), and a reafference of this increasing signal could enhance activity at the position of the saccade target.

An alternative possibility for the timing differences is an involvement of attentional processes. Attention is known to speed up visual processing at the attended area. Shortly before a saccade, attention shifts from the fixation point to the saccade target (Deubel and Schneider, 1996). Therefore, both the fixation point and the saccade target area may benefit from attentional speed up while the more distant parts of the visual field would show slower processing.

Transient perisaccadic changes in receptive field properties or firing behavior of neurons may underlie

perceptual mislocalization. They have been described in a number of brain areas (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997; Tolia et al., 2001; Krekelberg et al., 2003). In particular, perisaccadic receptive field shifts orthogonal to saccade direction have been reported in macaque area V4 (Tolia et al., 2001). It would be interesting to see whether these orthogonal shifts occur for the same spatial receptive field positions as found in our experiments. If the process of mislocalization correlates with remapping, as proposed in our model, an earlier start of mislocalization for positions nearer to the fixation point could be explained by an earlier remapping for these positions. Whereas remapping occurs over a considerable time span in various areas, to our knowledge, a correlation between the spatial position and the start of remapping has not been looked for. Electrophysiological experiments in LIP or V4, for example, that correlate receptive field positions with the time course of remapping could clarify our hypothesis.

#### Experimental Procedures

##### Subjects

Subjects were three males (30–38 years old; HF, HA, ML) with normal or corrected vision. One of the subjects (ML) was an author of this study. The saccadic latencies, i.e., the times between stimulus presentation and saccade onset, were on average 135–170 ms for the different subjects.

##### Stimulus Presentation

Subjects sat in a dimly lit room 40 cm in front of a 19 inch monitor (Samtron 95P plus, visible screen area of 36.6 cm × 27.5 cm, or 49.2° × 37.9°, respectively), with the head supported by a chin rest. The subject was placed directly in front of the center of the screen. Screen images had a resolution of 800 × 600 pixels and were presented at a frame rate of 85 Hz. Throughout the experiment, the screen displayed a black ruler on a red background (luminance 13 cd m<sup>-2</sup>). In each trial, first a fixation point at position (0°, 0°) was presented for 500–1500 ms. Then, the fixation point disappeared, and the saccade target was shown for 50 ms at target position. The subject was instructed to make a saccade toward the target as quickly as possible. At a random point in time up to 300 ms later, a green dot (luminance 43 cd m<sup>-2</sup>; diameter 1.2°) was presented for one video frame (12 ms). Its position was chosen pseudorandomly from a grid of possible positions. After 500 ms, a mouse pointer became visible and was used by the subject to report the perceived position of the dot by mouse click. The position of the target and the possible dot positions were varied following the setup for three experiments.

##### Horizontal 20° Saccade

A saccade was made from left to right where the saccade target had the coordinate (20°, 0°) relative to the fixation point (Figure 3A). The 24 possible dot positions were arranged in a grid around the target position with spacing of 4°.

##### Vertical 20° Saccade

Subjects performed a downward 20° saccade. Four possible dot positions were arranged on an 16° × 16° square centered on the saccade target (Figure 5A). A vertical ruler was continuously visible.

##### Horizontal 24° Saccade

The position of fixation point and grid of dot positions was the same as for the horizontal 20° saccade (Figure 6A). The only difference was that the target was presented at position (24°, 0°) while a possible dot position was at (20°, 0°).

##### Horizontal 12° Saccade

The position of fixation point and grid of dot positions (Figure 6C) was the same as for the horizontal 20° saccade except that the target was presented at position (12°, 0°) while a possible dot position was at (20°, 0°).

##### Horizontal 16° Saccade

The position of fixation point and grid of dot positions (Figure 6E) was the same as for the horizontal 20° saccade except that the target was presented at position (16°, 0°) while a possible dot position was at (20°, 0°).

##### Data Analysis

Eye position was measured with a video-based eye tracker (SMI Eye-Link) at a sample rate of 250 Hz. The start of the eye movement was determined by a velocity threshold of 35°/s. Data analysis and graphics were prepared using Mathematica. Each trial was checked for correct saccade, i.e., whether the timing was correct and whether the endpoint of the saccade was near ( $\leq 2^\circ$ ) the saccade target. Trials with incorrect saccade were discarded, as were rare trials in which the subject did not perceive the flashed dot. Dot presentation times with respect to saccade onset were calculated on a trial-by-trial basis from the saccade latency and the presentation times of the dot. Onset times of the mislocalization for a specific dot position were determined by finding the point in time at which the mislocalization effects were half-maximal relative to the baseline. The baseline was calculated as the average perceived position for dots presented more than 90 ms before or 70 ms after the start of the saccade.

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