

The effect of optokinetic nystagmus on the perceived position of briefly flashed targets

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Abstract

Stimuli flashed briefly around the time of an impending saccade are mislocalized in the direction of the saccade and also compressed towards the saccadic target. Similarly, targets flashed during pursuit eye movements are mislocalized in the direction of pursuit. Here, we investigate the effects of optokinetic nystagmus (OKN) on visual localization. Subjects passively viewed a wide-field drifting grating that elicited strong OKN, comprising the characteristic slow-phase tracking movement interspersed with corrected "saccade-like" fast-phase movements. Subjects reported the apparent position of salient bars flashed briefly at various positions on the screen. In general, bars were misperceived in the direction of the slow-phase tracking movement. Bars flashed around the onset of the fast-phase movements were subject to much less mislocalization, pointing to a competing shift in the direction of the fast-phase, as occurs with saccades. However, as distinct from saccades, there was no evidence for spatial compression around the time of the corrective fast-phase OKN. The results suggest that OKN cause perceptual mislocalizations similar to those of smooth pursuit and saccades, but there are some differences in the nature of the mislocalizations, pointing to different perceptual mechanisms associated with the different types of eye movements.

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1. Introduction

When viewing their surroundings, primates use a combination of saccadic and pursuit eye movements in order to centre and stabilize the retinal images of objects of interest. Saccades are discrete ballistic eye movements that frequently reposition our gaze, translating the image of the object of interest from an eccentric retinal location to fovea. Smooth pursuits are continuous eye movements that keep the image of moving objects centred on the fovea. But despite these movements, the world remains substantially stable, showing that compensatory mechanisms generally work well. However, despite (or perhaps because of) these

compensatory mechanisms, a number of systematic errors occur in locating transiently displayed stimuli.

When subjects are asked to report the position of a target flashed just prior to a saccade, they mislocate it, primarily in the direction of the saccade (Honda, 1989; Mateeff, 1978; Matin & Pearce, 1965). Typically, localization errors start up to 100 ms before saccadic onset and are maximal at saccadic onset. More recent studies, however, have shown that in addition to the shift in saccadic direction, there is a gross perceptual compression of visual space (Lappe, Awater, & Krekelberg, 2000; Matsumiya & Uchikawa, 2003; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). The size and even the sign of errors depend strongly on the position in the visual field, causing spatial compression. All the data can be well described by a compression towards the fovea, and a shift of the compressed image in the direction of saccadic goal, both proceeding smoothly

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over time (see Morrone et al., 1997 for full mathematical details). Under some circumstances, the compression can be so strong as to cause the mislocalization of the saccade target towards the position of stimuli flashed around the time of the saccade (Awater & Lappe, 2006; Morrone, MaWyatt, & Ross, 2005).

Peri-saccadic compression of space is a general phenomenon, observable in most data collected both in the light and in darkness (Matin & Pearce, 1965; e.g. Bischof & Kramer, 1968; cf. Awater & Lappe, 2006; Lappe et al., 2000). It also occurs in the absence of visual references when relative distance from saccadic target is considered. Experiments with anti-saccades (Awater & Lappe, 2004) and saccadic adaptation (Awater, Burr, Lappe, Morrone, & Goldberg, 2005) suggest that compression is directed towards the landing point of the eyes, rather than towards the visual cue that evoked the saccade. As both the compression and the displacement of transient stimuli follow very similar time course, both similar to that of saccadic suppression (see Ross, Morrone, Goldberg, & Burr, 2001), it is generally accepted that they all result from a similar neural mechanism, in the form of a *corollary discharge* or *efference copy*.

Spatial mislocalization of transiently displayed stimuli also occurs with smooth pursuit motion. When a target is flashed during a pursuit eye movements it is seen displaced towards the direction of the movement (Brenner, Smeets, & van den Berg, 2001; Mateeff, Yakimoff, & Dimitrov, 1981; Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979). Mitrani et al. (1979) and Mateeff et al. (1981) found that the localization bias was smaller when the target appearance was predictable. However, Rotman, Brenner, and Smeets (2002) suggested that the spatial position of the stimulus was more important in reducing mislocalization. In a more recent experiment, Rotman, Brenner, and Smeets (2004) found that the systematic mislocalization is related to the movement of the eyes, rather than to the movement of the pursued target, and determined more by the movement after the flash than before it. Interestingly, also for pursuit movements the mislocalization is not uniform across space, but there is a slight expansion of visual space away from the fovea (Kerzel, Aivar, Ziegler, & Brenner, 2006). Unlike the visual compression that accompanies saccades, the amount of expansion during pursuit was not affected by target luminance or contrast.

It has been suggested that the shift in the direction of the pursuit eye movements could result from efferent eye position information. The efference copy of the eye movement command always specifies a position that is a bit further than where the eyes are. Therefore, combining this with retinal information will cause a mislocalization in the direction of the eye movement (similar to the ideas espoused to explain peri-saccadic mislocalization). Although smooth-pursuit movements and saccades are controlled by different neural structures, the similarities in the mislocalizations caused by the two types of movement agree well with the recent idea the two systems have a similar functional architecture (Krauzlis, 2004).

Overall these studies have concentrated on purposeful movements of the eyes, that position or maintain gaze on

an object of interest. Our purpose here is to examine spatial localization during optokinetic nystagmus (OKN, a reflexive ocular motor response is elicited by large-field motion), in order to investigate the importance of conscious *intention* of eye movements in causing mislocalizations. Although some degree of control over the amplitude and frequency of OKN is possible, they are somewhat less voluntary than saccades and pursuit eye movements. OKN has two rhythmic components: a *slow-phase* eye movement in the direction of motion stimulation (resembling smooth pursuit) and a *fast-phase* resetting the eyes in the opposite direction (resembling saccades). In this study, we ask how visual localization is influenced by these two components of OKN, considering that previous studies have shown specific and separate effects of the two systems.

Similar results have been reported by Kaminiarz and colleagues, both as conference proceedings (Kaminiarz, Rohe, Krekelberg, & Bremmer, 2006) and in a companion paper in this issue (Kaminiarz, Krekelberg, & Bremmer, 2007), to which the interested reader is referred. The results complement nicely those presented here, in that they study the effects of OKN in two-dimensional space. A short report of the present study has been published as conference proceedings (Tozzi, Morrone, & Burr, 2005).

2. Methods

2.1. Stimuli

Stimuli were salient blue bars ($1^\circ \times 68^\circ$) superimposed on a sinusoidal grating of 0.2 c/deg (30% contrast), generated by a frame-store (Cambridge Research System VSG 2/5) and displayed on the face of a Barco monitor at 120 Hz (see Fig. 1b). The CIE coordinates for the bar and background were, respectively: $x = 0.14$, $y = 0.07$, $Z = 6 \text{ cd/m}^2$; $x = 0.32$, $y = 0.35$, $Z = 36 \text{ cd/m}^2$. The display area was $91 \times 68^\circ$ at the viewing distance of 25 cm. To stimulate OKN, the grating was drifted leftwards at a speed of 10 deg/s. The time of presentation of the bar was determined by computer and displayed to the experimenter, together with the eye movement trace, after each trial, with a visual display (see Fig. 1a).

2.2. OKN

Eye movements were measured using an infra-red video-based eye tracking device, sampling at 240 Hz with a transport delay of about 12 ms (ASL C6-HS). The resolution was 0.5° , and accuracy was 0.1° (manufacturer's specifications). The optics was mounted above the eye with a infra-red reflecting mirror monacle below the right eye. The PC sampled eye position at 1000 Hz and stored the trace in digital form (after suitable linearization). Before each session, the linearization of the eye tracker was calibrated by asking observers to look at nine target points that covered about 80% of the monitor screen area. Calibration was checked frequently during the recording sessions.

2.3. Procedure

Observations were made in a darkened room. The participant's head rested on a chinrest to help minimize head movements. Optokinetic nystagmus was elicited by stimulating the visual field with a low-frequency sinusoidal grating on a large screen. The subjects sat in front of the screen and were instructed not to follow intentionally the movement with the eye, but to watch the screen in a relaxed manner, passively viewing the grating and allowing the optokinetic reflex to control the eye movements ("stare" OKN). This stimulus elicited strong OKN, comprising slow tracking phases

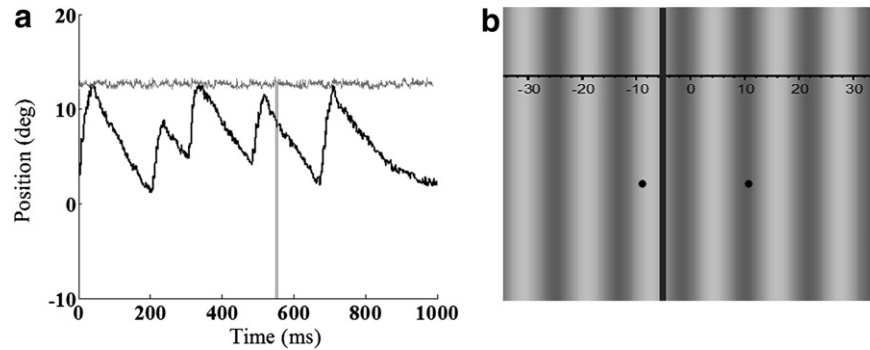


Fig. 1. (a) One-second registration of an optokinetic time series (black). Upwards represents eye movements to the right, downwards to the left. The stimulus bar (indicated by the grey line which was actually blue) could be displayed at any position. (b) The optokinetic stimulation consists of vertical stripes moving with a velocity of 10 deg/s to the left. Fixation point at -10° and target point at $+10^\circ$ are presented only for voluntary saccade (following a specific time course, see Section 2) or for fixation condition (one at a time presented). The vertical grey bar is the stimulus.

interspersed with fast saccade-like corrective movements. In the voluntary saccades condition, trials began with a dark fixation spot (0.5°) superimposed on the moving OKN stimulus, which appeared 10° to the left of the centre of the screen and stayed on thereafter. After a warning a dark spot appeared (and stayed on) 10° to the right of the centre, and observers made a saccade to it as soon as they could. Latencies for voluntary saccades to appear varied with observer within a range of 160–220 ms. In fixation condition, subjects had to localize the bar while fixating a point (0.5°) superimposed on the OKN stimulus 10° to the right or to the left of the centre of the screen. Stimuli were flashed for one frame (8 ms) some time after the appearance of the target and could fall before, during, or after fast-phase OKN or voluntary saccade. Subjects, who were unaware of actual display positions, reported where bars appeared with reference to a ruler that was displayed continuously 30° above gaze. They could observe the ruler from time to time to remain calibrated, but it was too far from the line of gaze to be resolvable during eye movements. Subjects voiced their responses, which were recorded by an experimenter. The arrangement of fixation point, saccade target, ruler and bar are shown in Fig. 1b.

2.4. Data analysis

An offline program analysed the data identifying the beginning of the fast-phase OKN or voluntary saccade, and calculated the delay of the stimulus presentation (positive or negative) relative to saccadic onset. The experimenter checked manually that the onset of fast-phase had been identified correctly. For OKN trials the program also reported eye position during the appearance of the bar, the onset and the offset of the fast-phase OKN. The eye movement data were analysed during both OKN and saccade runs. The OKN were analysed to eliminate two types of trials: trials in which voluntary saccades were made during bar presentation (in order to remove contamination of voluntary movements from reflexive movements), and trials in which the fast-phase OKN was less than 5° . In the voluntary saccade experiment, trials were aborted if the saccade was inaccurate ($>0.3^\circ$ from target), or if there were double-step or corrective saccades. Each subject performed each condition in different sessions of 30 trials, resulting in a total number of about 350 per condition.

2.5. Observers

Observers included two of the authors and a student naïve to the goals of the experiment. All had normal or corrected-to-normal vision.

3. Results

3.1. Effect of voluntary saccades on apparent position

Before measuring the effects of OKN on spatial localization, we first established that we were able to replicate our

previous results with saccadic eye movements under the particular conditions of our experiment including the presence of a fast-moving background grating. Here subjects fixated a clear fixation point 10° left of screen centre, superimposed on a low-frequency grating drifting leftwards at 10 deg/s. On warning they saccaded to a target 10° right of screen centre. Bars were flashed for one frame at various positions on the screen, and over a wide range of times, ranging from well before (<-150 ms) to well after (>150 ms) the start of saccade. The results for two observers, reported in Fig. 2, replicate well the characteristic shift and compression normally found under these conditions. Bars displayed at positions -20° and 0° were displaced in the direction of the saccade, while those displayed at 20° were displaced in the opposite direction, to cause a

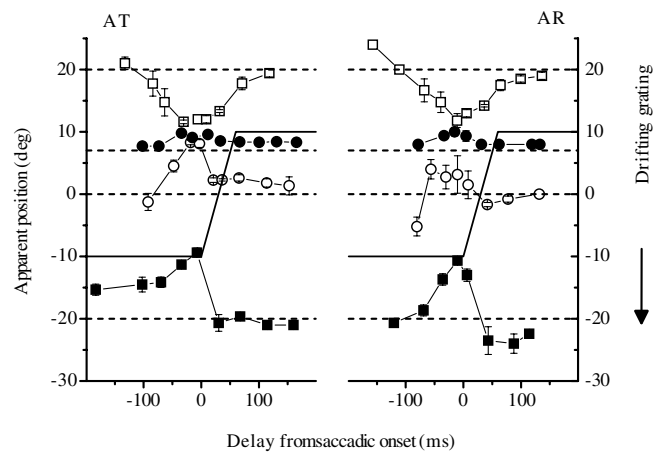


Fig. 2. Apparent position of bar flashed at various times relative to saccadic onset. Observers AT and AR saccaded from the fixation point at -10° (10° left of screen centre) to the target at 10° , while a grating drifted across the background at 10 deg/s. The bars were displayed briefly to one of four possible positions: -20° (close squares), 0° (open circles), 7° (close circles), or 20° (open squares). There were no systematic errors in the direction of the drifting grating. Bars displayed to the left of the saccadic target were mislocalized in the direction of the saccade, with maximum error just before saccadic onset; bars displayed past the target were mislocalized in the other direction, toward the target. The continuous lines show eye position trajectories, dashed lines the physical positions where targets were flashed.

compression around the saccadic landing point at 10° . Bars displayed near the position of the saccadic target were seen fairly veridically. The curves for all bar positions show the characteristic dynamics, beginning to be mislocalized 100 ms or so before saccadic onset and showing maximum mislocalization at saccadic onset.

Fig. 3 shows the results of the third observer, for whom data was collected for many spatial locations, to show the effect of saccades as a function of space. The filled squares show position judgements for bars presented in the interval of -40 to -20 ms, the critical interval where effects are large-

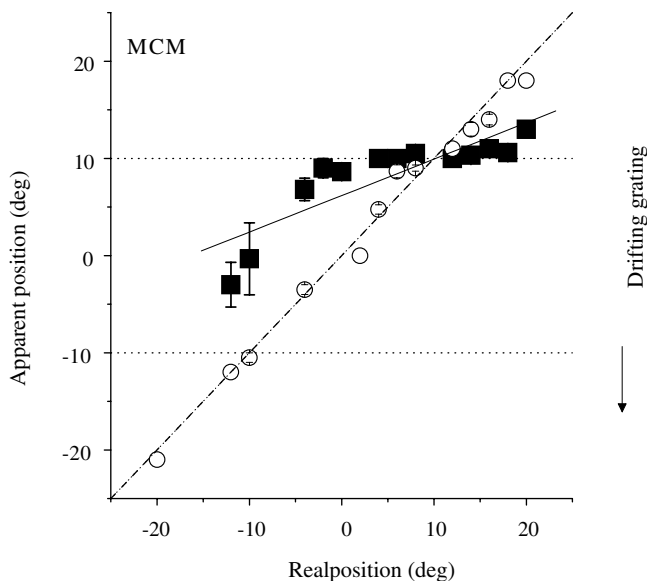


Fig. 3. Perceived position of bar flashed over a range of spatial positions as observer MCM saccaded from the fixation point at -10° to the target at 10° over a background grating drifting leftward. Filled square times show data for bars presented within the range of -40 to -20 ms, saccadic onset, *open circles* data outside this range (<-60 or >20 ms). The dashed diagonal line indicates veridical position, the continuous line the best linear fit to the data. The slope of this regression (that accounts for 72% of the data) is $0.37 (\pm 0.07)$.

est. Again the results replicate well previously reported findings, showing a clear compression towards the saccadic target: all bars presented in the 20° region around the saccadic target tended to be seen in a similar position. The open circles show data for bar presentation outside this critical interval (<-60 ms or >20 ms), showing that these stimuli are seen veridically. Other data for this observer on this experiment are shown in Fig. 7d, and will be described later.

3.2. Effect of OKN on perceived position

We next measured the effects of OKN by having observers view passively the drifting grating without fixation spot. This condition elicited strong OKN, comprising slow tracking phases interspersed with fast saccade-like corrective movements. Fig. 1a shows a typical recording trace. At a random interval after a warning tone, long salient bars were flashed briefly at various positions on the screen, superimposed on the drifting grating. Subjects, unaware of actual display positions, reported where bars appeared with reference to a ruler that was continuously displayed well above eye gaze (see Fig. 1b). In another condition, subjects fixated a fixation spot and localized the positions of the briefly displayed bars.

Fig. 4 shows the results of this experiment for all three observers, plotted as a function of time of bar presentation relative to fast-phase onset. For all observers, the bars tended to be seen displaced leftwards, in the direction of the slow-phase tracking movement. However, the magnitude of the displacement depended critically on the stimulus presentation time. For bars displayed well before or well after the onset of the fast-phase, the shift was about 5° in the direction of the grating drift. However, for a period from about 100 ms prior to fast-phase onset till onset (-100 to 0 ms) the displacement reduced considerably, approaching veridicality. The horizontal dotted line in Fig. 4 shows an estimate of this baseline shift, measured midway during the slow-phase of the OKN. The effects were qualitatively similar for all observers, although there were differences in magnitude.

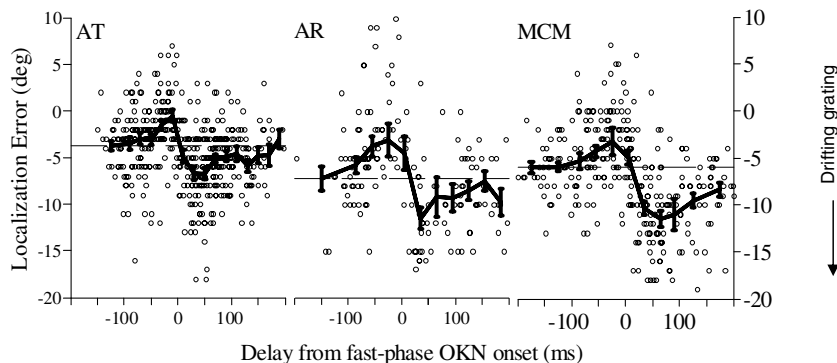


Fig. 4. Localization error of a bar flashed briefly (8 ms) at various positions, as observers passively viewed a screen on which was displayed a grating drifting leftward at 10 deg/s (indicated by the arrow on the right). The abscissa shows the presentation time relative to onset of the fast-phase of OKN. (Only trials where the fast-phase was greater than 5° are included). The physical position of the bar was between -20° and $+30^\circ$ of the subject's gaze position. The filled points joined by the heavy curve show the average data within a bin (bin edges midway between points), with error bars showing standard error of the averages. The pattern of results for the three subjects was very similar. Bars were generally mislocalized in the direction of slow-phase OKN, but the mislocalization was modulated by the fast-phase OKN, so it was less at the start of saccades.

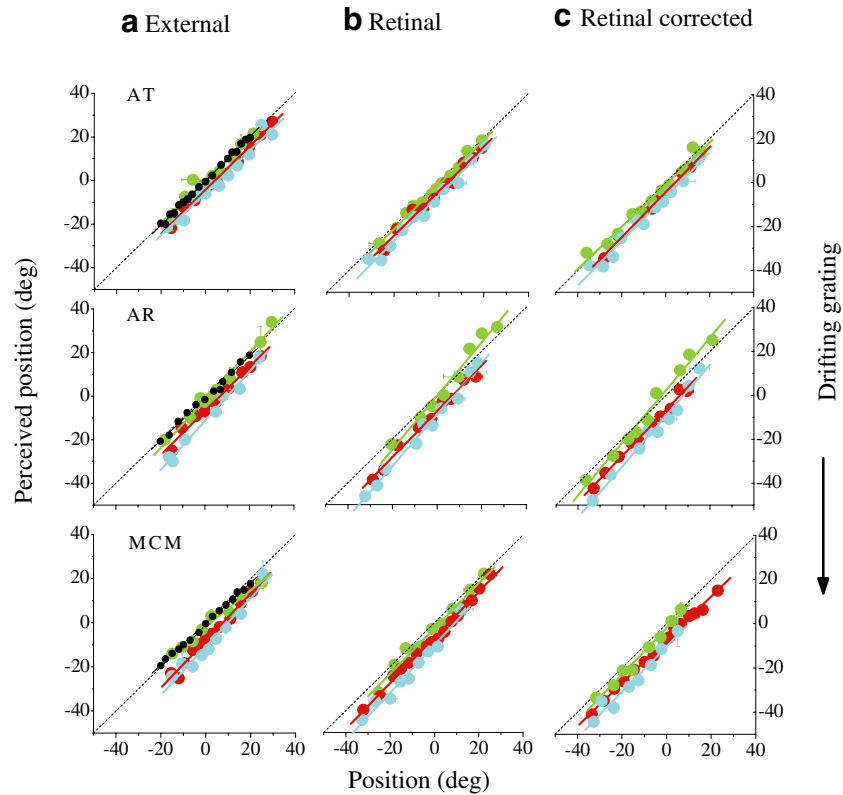


Fig. 5. Perceived position of bars presented at various positions relative to external (a), retinal (b) and corrected-retinal coordinates (c) for the three observers. In all cases the data were binned into three different groups on the basis of bar presentation time relative to fast-phase onset, individually for each subject. *Slow-phase* trials ($t < -100$ ms for AT and MCM, and $t < -80$ ms for AR) are indicated by red symbols, *fast-phase onset* by green symbols ($-30 < t < -10$ ms for AT, $-30 < t < 0$ ms for AR and $-40 < t < -20$ ms for MCM), and *fast-phase offset* by cyan symbols ($30 < t < 60$ ms for AT, $30 < t < 50$ ms for AR and $40 < t < 80$ ms for MCM). Black symbols show control trials during fixation (at one of the fixation points). The *continuous coloured lines* show the best linear fit. The *dashed lines* show the prediction for veridical perception. In curves (a) the abscissa shows the bar position in screen coordinates, and the ordinate the reported bar position; in (b) the abscissa is bar position in retinal coordinates (screen coordinates minus eye position) and the ordinate has the same correction; in (c) the abscissa reports the bar position relative to fast-phase OKN landing position, with the ordinate having the same correction. The slopes of the best fitting linear regressions (for the external coordinates) were 1.02 ± 0.02 for the slow-phase data, 0.96 ± 0.08 for fast-phase onset and 1.07 ± 0.05 for fast-phase offset, all virtually identical.

To understand better the effect of spatial position on mislocalization, we divided the data on the bases of presentation time relative to fast-phase onset, and plotted these results separately as a function of position (Fig. 5). The actual parameters for the binning were chosen individually for the three subjects on the basis of the dynamics shown in Fig. 4 (see caption of Fig. 5 for details). However the divisions always correspond to trials just prior to fast-phase onset (green symbols of Fig. 5), trials just before fast-phase offset (cyan symbols), and trials distant from the fast-phase (red symbols). The control trials measured during fixation are shown with small black symbols.

The curves at left (Fig. 5a) show the data in screen coordinates, uncorrected for actual eye position. The fixation measurements fell near the equidistant line, confirming that observers had little difficulty with the task and that the passive action of the drifting grating had little effect on bar localization (the average effect was 0.5° in the direction of motion for observers AR and MCM, and virtually 0 for AT). The trials during the slow-phase (red symbols) confirm the effect shown in Fig. 4 that during slow-phase OKN

there is a shift of the perceived position in the direction of the drift. The magnitude of the shift varied from subject to subject, from about 4° for AT to 8° for AR and MCM. For each subject, the amount of shift did not depend on position of the bar on the screen, as shown by the fact that the linear regression had unity slope, virtually parallel to the equidistant line. The unity slope means there was no compression or expansion of visual space during this period. For presentations just before fast-phase onset (green symbols), the perceived position tended towards veridicality, as was evident also in Fig. 4. But again, there was no tendency for the results to depend on spatial position of the bar. A compression, as occurs with saccades would cause the slope to be considerably less than 1, like that of Fig. 3. But the slopes were never significantly different from 1, for any observer, for any correction for eye position (see caption of Fig. 4 for regression values).

There are several necessary differences in the techniques used to study the effects of OKN and voluntary saccades on perceived position. One is that saccades are typically made from a fixed position on the screen to another, whereas with

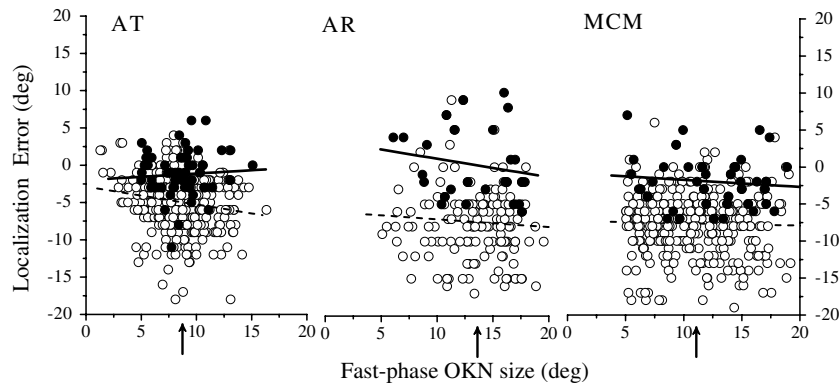


Fig. 6. Localization error against size of the fast-phase OKN movement for three observers. Filled circles show trials near the fast-phase OKN onset ($-30 < t < -10$ ms for AT, $-30 < t < 0$ ms for AR and $-40 < t < -20$ ms for MCM) with the continuous lines showing linear regression. The open circles show data from other presentation times, with regression shown by dashed lines. None of the slopes of the regression lines was significantly different from zero. The arrows on the abscissa indicate mean size of fast-phase movements for each subject (note that all movements less than 5° have been excluded from this and all other analyses).

OKN the position of gaze varies unpredictably with each stimulus presentation. Another difference is that the amplitude of OKN fast-phases vary considerably, whereas saccades are usually of a fixed amplitude in any experimental condition. We therefore examined the results as a function of retinal rather than screen position, to see if it would reveal any sign of compression otherwise masked by this randomness. Fig. 5b replots the data of Fig. 5a in retinal coordinates (subtracting eye position from the position of the bar in screen coordinates). The responses (ordinate) were also corrected in the same way, so any deviation from the equality line represents localization error. This correction had virtually no effect on the pattern of results. Measurements during the slow-phase were mislocalized as before, and this mislocalization reduced during the fast-phase. But importantly, the slopes of the curves all remained statistically indistinguishable from unity, indicating no compression.

It maybe argued that it is not retinal position at fast-phase onset that is important, but the position at offset, at the landing position (analogous to the saccadic landing position). In the saccade experiment saccadic landing was always a fixed distance from fixation, and compression was seen around this point. With OKN, however, the fast-phase “saccades” are of variable amplitude so this relationship does not hold. The data of Fig. 5c are therefore plotted in retinal coordinates relative to fast-phase “landing”. That is to say, the position of the eye at the end of the fast-phase was subtracted from the position of the bar on the screen, and the same correction was applied to the reported results. Again, there was no evidence of peri fast-phase compression, that would have caused a decrease in slope of the regression passing through the green data points.

Could it be that the results are confounded by the size of the fast-phase “saccades”? As mentioned earlier, only fast-phase corrections greater than 5° have been considered in this analysis. But to examine further the effect of eye movement amplitude, Fig. 6 plots the localization errors against amplitude of fast-phase OKN for the three subjects. Filled

symbols show results for bar presentation near fast-phase onset, open symbols other times. Although the average amplitude (indicated by arrows on the abscissae) varied somewhat from subject to subject, localization errors showed no strong dependency on saccadic size. Indeed none of the regression lines was significantly different from zero.

In a final attempt to reveal evidence for compression we divided all the data into three groups, based on the position of the bar relative to fast-phase or saccadic landing (left, right or centre), and plotted localization error for these as a function of time relative to fast-phase onset. Fig. 7a–c shows the results for the three subjects. Bars flashed to the left of fast-phase or saccadic landing are shown as filled squares, those to the right as open circles (centre presentations not plotted). There is no evident difference between the two groups of data during the critical period near the start of the fast-phase movement. Both show a baseline negative localization error (in the direction of the grating drift) that reduces to near zero near the onset of the fast-phase movement. There is a slight difference in the data after the fast-phase movement for two subjects, but nothing like the behaviour observed during voluntary saccades, illustrated for MCM in Fig. 7d. There the pattern of mislocalizations is exactly opposite for the two sets of spatial presentations. Stimuli presented to the left of the screen were mislocalized in the direction of the saccade (upwards in Fig. 7), those to the right of the screen in the opposite direction. This is the clear signature of compression (like that shown in Fig. 3), completely lacking in the data collected during OKN.

4. Discussion

This paper examined visual localization during OKN eye movements, revealing three primary facts:

1. During the slow-phase, transiently presented bars are mislocalized in the direction of the drift, similar to the

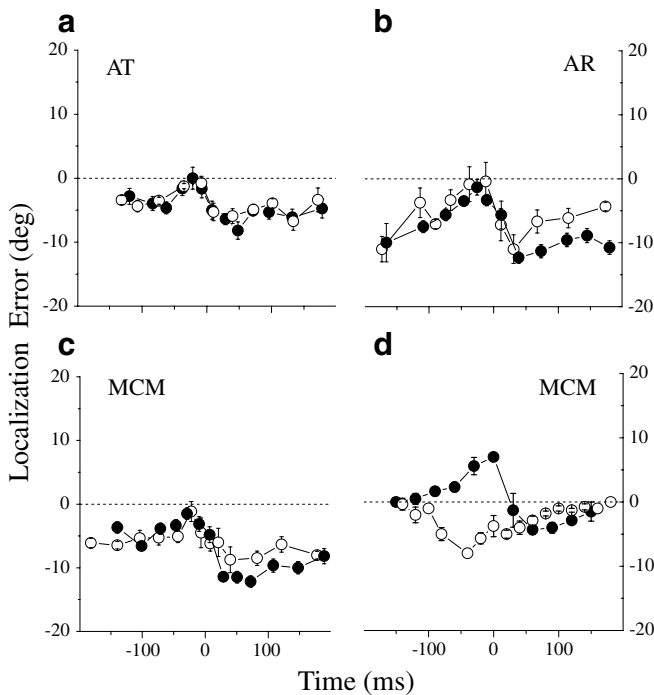


Fig. 7. (a–c) Localization errors during OKN eye movements for three observers. Open circles show trials in which the bar was displayed to the right of the fovea, filled circles bar at the left. (d) Errors in location during voluntary saccades, with data divided in a similar way and indicated by the same symbols.

results obtained with voluntary smooth-pursuit movements.

2. Near the onset of the fast-phase of OKN, the mislocalization is greatly reduced, implying a competing shift in the direction of the fast-phase, as occurs with voluntary saccades.
3. As distinct from voluntary saccades, we found no evidence for spatial compression around the time of the corrective fast-phase OKN.

Trials under conditions of fixation suggested that the image motion itself had effect on perceived position, about 0.5° at most, less than 10% the size of the effects produced by OKN. While this result may seem at variance with other studies that have shown that motion can affect the apparent position of flashed stimuli (Whitney & Cavanagh, 2000), even for stimuli distant from the moving source, it is in fact quite consistent. Compared with the mislocalizations reported here, the effects of Whitney and Cavanagh are small, about 0.3° at most, similar to those we find in our control condition. However, the reader is also referred to the companion paper by Kaminiaz et al. (2007), who report a larger effect under conditions of fixation. Perhaps the difference derives from the different stimuli, small spots rather than extended bars.

Experiments with voluntary saccades show that the presence of the background drifting grating did not in itself produce a mislocalization, nor did it reduce the compressive effects, that were essentially the same as other reported

data (Burr, Morrone, & Ross, 2001; Lappe et al., 2000; Morrone et al., 2005, 1997; Ross et al., 1997).

Although there are some differences in optimal stimuli and responses of OKN and smooth pursuit, it is generally considered that they are controlled by similar neural mechanisms (Heinen & Keller, 2004). This has recently been confirmed in humans with an fMRI study (Konen, Kleiser, Seitz, & Bremmer, 2005). Furthermore, Krauzlis (2004) has recently shown that the pursuit system has functional architecture very similar to that of saccadic system, so the three different types of eye movement are perhaps not as functionally separate as previously thought.

The effects of the slow-phase of OKN on target localization were similar to those that have been observed for pursuit movements, except they were greater in magnitude. The average mislocalization during the slow-phase of OKN was 8° for two observers and 4° for the other. With smooth pursuit, the magnitude of mislocalization depends on many things including target predictability, background patterning and target speed (Brenner et al., 2001; Kerzel et al., 2006). However, under optimal conditions (14 deg/s with a structured background), the maximal localization errors are about 3.5° , somewhat less than the average errors reported here.

The shift before the fast-phase showed dynamics that were reasonably similar to those observed during voluntary saccades. During saccades, the maxima tend to occur at the saccadic onset, whereas here the tendency was for the peak to occur slightly earlier than fast-phase onset. However, given the difficulty in collecting data during OKN and the resultant variability, it would be incautious to place too much emphasis on this small difference. Although there was considerable variation in the amount of shift from trial to trial and between subjects, the average maximum shift against the pursuit shift was about 4° . With saccades the maximum shift tends to be about half the saccade magnitude. As the average magnitude of the fast-phase movements was about 10° (varying from observer to observer), the magnitude of the average shift is consistent with that found with saccades. However, for the OKN study, we found no significant dependency on size of fast-phase movements (filled symbols of Fig. 6). There may be many reasons for this: there was much variability in the data, with few trials falling in this crucial period. In addition, these are not isolated eye movements, but made to correct the slow-phase drift, which itself causes mislocalization in position. It may well be that this complication masks any potential dependencies on eye movement magnitude.

Importantly, our data revealed no compression of visual space near the fast-phase of OKN, suggesting that compression is peculiar to saccades. This is not altogether expected, as previous studies have shown that during a saccadic adaptation paradigm, compression occurs towards the point of saccadic landing, not the original intentional target (Awater et al., 2005). One possible reason for the failure to see the compression may be that the technique was not sensitive enough to observe it. This seems unlikely, as the compression is usually very robust, and was easily

measured under the conditions of this study (Figs. 2, 3, and 7d). It is possible that the effects of the slow-phase motion, shifting apparent position in the other direction, somehow disguised the compression, but it is not at all obvious how or why this should occur. Possibly the slow-phase produced a perceptual expansion that somehow counteracted the compression (although this does not seem feasible, as there was no evidence for either when the data were appropriately separated). The most probable explanation is that the compression is related to the intentional movement towards a given goal, and does not occur for nystagmic reflexes. This would suggest that, at least as far as their perceptual consequences are concerned, saccades differ from OKN fast-phase movements.

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