

Moving your head reduces perisaccadic compression

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Flashes presented around the time of a saccade appear to be closer to the saccade endpoint than they really are. The resulting compression of perceived positions has been found to increase with the amplitude of the saccade. In most studies on perisaccadic compression the head is static, so the eye-in-head movement is equal to the change in gaze. What if moving the head causes part of the change in gaze? Does decreasing the eye-in-head rotation by moving the head decrease the compression of perceived positions? To find out, we asked participants to shift their gaze between two positions, either without moving their head or with the head contributing to the change in gaze. Around the time of the saccades we flashed bars that participants had to localize. When the head contributed to the change in gaze, the duration of the saccade was shorter and compression was reduced. We interpret this reduction in compression as being caused by a reduction in uncertainty about gaze position at the time of the flash. We conclude that moving one's head can reduce the systematic mislocalization of flashes presented around the time of saccades.

Introduction

Flashes that are presented around the time of a saccade are systematically mislocalized. Two components of this mislocalization have been identified: a shift of the flash's apparent location in the direction of the saccade (Bischof & Kramer, 1968; Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1990, 1991; Mateeff, 1978; Matin, Matin, & Pola, 1970; Matin & Pearce, 1965; Schlag & Schlag-Rey, 2002) and a spatial compression of the flash's apparent location toward the saccade

target location (Awater, Burr, Goldberg, Lappe, & Morrone, 2001; Honda, 1993; Lappe, Awater, & Krekelberg, 2000; Maij, Brenner, & Smeets, 2009; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997) or toward the endpoint of the saccade (Awater & Lappe, 2004; Matziridi, Brenner & Smeets, 2013; Matziridi, Hartendorp, Brenner, & Smeets, 2014). This perisaccadic compression has been partially attributed to uncertainty about the orientation of gaze at the time of the flash (Brenner, Mamassian, & Smeets, 2008; Brenner, van Beers, Rotman, & Smeets, 2006; Maij et al., 2011a; Matziridi et al., 2014). The compression has been found to increase with the amplitude of the saccade (Lavergne, Vergilino-Perez, Lappe, & Doré-Mazars, 2010) and with its peak velocity (Ostendorf, Fischer, Finke, & Ploner, 2007).

In most studies on perisaccadic mislocalization, the head does not contribute to the gaze shift, so the gaze shift corresponds with the rotation of the eyes relative to the head (eye-in-head rotation). Moving the head during the gaze shift will reduce eye-in-head velocity and amplitude (Tabak, Smeets, & Collewijn, 1996) and might therefore be expected to decrease uncertainty about the orientation of gaze (Saglam, Lehnert, & Glasauer, 2011) and thereby presumably the amount of compression (assuming that uncertainty about the orientation of the eyes is not negligible with respect to uncertainty about the time of the flash; see Brenner & Smeets, 2010). However, a study by Richard, Churan, Guitton and Pack (2011) suggests that if anything, moving the head during a saccade increases compression. Since that study used very large saccades, for which compression was almost complete during the gaze shifts irrespective of the precise amplitude and of the extent to which head movements contributed, we

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decided to re-examine this issue with smaller saccades. We asked participants to shift their gaze between two positions, either without moving their head or with the head contributing to the change in gaze. We flashed bars around the time of the saccades and asked participants to indicate where they saw these bars. For the second half of the saccade, we found less compression when part of the change in gaze was achieved by rotating the head.

Methods

Participants

Eight participants (age: 29 ± 2 years; five women, three men) volunteered to take part in this study. All of them were unaware of the aim of the study and gave written informed consent prior to participation. Six of them were right-handed and two were left-handed. All of them had normal or corrected-to-normal vision. The study is part of a research program that has been approved by the ethics committee of the Faculty of Human Movement Sciences (ECB 2006-02).

Apparatus and experimental setup

The experiment was conducted in a normally illuminated room (fluorescent lamps). The participants sat in front of a touch screen (Elo Touch CRT 19-in., 800×600 pixels, 36×27 cm, 100 Hz) on which visual stimuli were presented using the Psychophysics Toolbox (Brainard, 1997). Each participant performed two types of trials: head-static and head-moving. In the head-static trials, a chin rest was placed in front of the touch screen to keep the participant's head static and facing the screen at a viewing distance of 57.3 cm. At this viewing distance, 1 cm equals 1° of visual angle. In the head-moving trials the participant's head was not restrained. To maintain approximately the same viewing distance as in the head-static trials, the chin rest was not totally removed but slightly lowered, preventing the participant from moving closer to the screen than that. Participants were also instructed to try to maintain the same viewing distance by keeping their chin above the lowered chin rest.

Eye movements were recorded with an EyeLink II eye tracker (SR Research Ltd., Mississauga, Canada) using the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002). This system records eye position with a spatial resolution of about 0.2° and a temporal resolution of 500 Hz. To determine the precise timing of stimulus presentation on the screen in relation to the recorded eye movement, a 2° white dot was presented

on a black square ($2^\circ \times 2^\circ$) in the lower right corner of the screen. This dot was presented on the same frame as the flashed green bar. It was not visible to the participant, but a photodiode attached to the lower right corner of the screen measured the light from this dot and sent a signal to the parallel port of the EyeLink computer as soon as the dot appeared. This signal was recorded in the data file of the EyeLink computer, which allowed us to later know precisely when the green bar occurred in relation to the eye movement (Maij, Brenner, Li, Cornelissen, & Smeets, 2010). The green bar was flashed at different places on the screen, so its timing relative to that of the flash varied by a few milliseconds. No corrections were made for these timing differences between green bars presented at different places on the screen.

Stimuli and conditions

The stimuli consisted of a black (9 cd/m^2) fixation cross (0.5° length lines), a black saccade target (0.27° diameter dot), and a flashed vertical green bar ($0.22^\circ \times 2^\circ$, 94 cd/m^2 ; $\text{CIE}_{xy} = 0.30, 0.56$), all on a white background (125 cd/m^2 ; $\text{CIE}_{xy} = 0.28, 0.32$). In each trial, one fixation cross, one saccade target, and one bar were presented on the screen (Figure 1). The fixation cross was presented randomly at one of 20 possible locations on the screen. The saccade target was always presented 12° to the right of the fixation cross. The green bar was flashed 6° , 8.4° , 10.8° , 13.2° , or 15.6° to the right of the fixation cross, which is 50%, 70%, 90%, 110%, or 130% of the distance between the fixation cross and the saccade target. The bar's center was always at the same height as the fixation cross and the saccade target. We had 10 conditions: five flash locations and two types of trials (head-moving and head-static).

The experiment consisted of sessions of 400 trials. Each session was divided into two equal blocks, one for each type of trial. In the head-static blocks, participants held their head stable on the chin rest. In the head-moving blocks, participants were instructed to start each trial with their head oriented about 30° to the left of the fixation cross. They were free to move their head during the task. The purpose of having participants' heads oriented 30° to the left of the fixation cross at the beginning of each head-moving trial was to encourage them to move their head during the trial. Otherwise, they would make the 12° gaze shifts with eye movements alone. The order of the blocks was randomized.

Each block therefore consisted of 40 trials for each of the five bar locations. The 200 trials within a block were presented in random order, with the restriction that the same bar location was never presented on

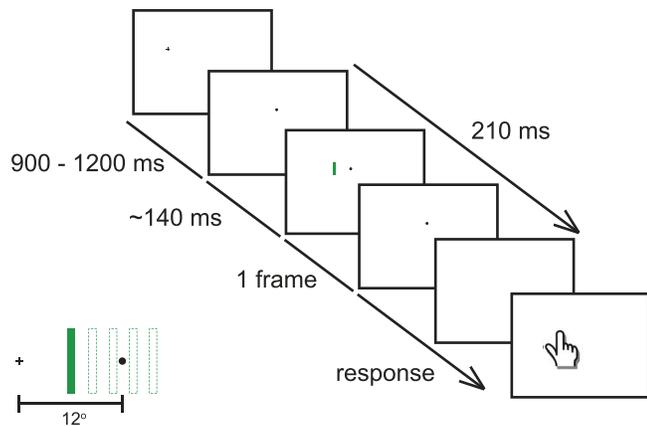


Figure 1. Schematic overview of an example trial. A fixation cross appears on the screen. After a random interval, it is replaced by a saccade target. Around the time at which the participant makes a saccade to the saccade target, a vertical green bar is presented at one of five possible locations for one frame (see inset, with a bar at 6° and dashed outlines at the other four locations). The participants had to indicate where they saw the green bar by touching that location on the screen with their index finger.

successive trials. The fixation cross was also never presented at the same location on successive trials. There was a short break between the two blocks of a session.

All participants performed at least 10 sessions of 400 trials. If 10 sessions did not yield enough successful trials to determine the mislocalization at each instant for each condition (see Mislocalization pattern, later), participants were asked to perform more sessions (with blocks of the relevant type) until we were able to make that determination. On average, participants performed 11 sessions.

Calibration

The touch screen was calibrated using the standard nine-point calibration provided by Elo Touch. The recording of the eye movements was calibrated using the standard nine-point calibration procedure of the EyeLink II. The head-movement compensation of the EyeLink was not reliable enough to deal with our large head movements (we found small systematic drifts in gaze when subjects fixated while moving their heads before and after saccades). We therefore relied on the eye-in-head data of the EyeLink (calibrated with the head static) and estimated the contribution of the head movement to the change in gaze on each trial on the basis of the eye's rotation during fixation, 36–16 ms before the saccade. We confirm that this estimate is reliable around the time of the saccade by plotting the changes in gaze that we calculated using this measure,

and checking that the gaze amplitude of the saccade is equal for the two head-movement conditions (see inset of Figure 2a). Note that our main analysis is based not on these estimates of gaze but on the eye-in-head measurements.

Procedure

A trial started with a fixation cross appearing on the screen (Figure 1). Participants had to fixate the cross with their head either static facing the center of the screen or oriented about 30° to the left of the fixation cross. After a random interval of 900–1200 ms, the fixation cross disappeared and the saccade target appeared on the screen for 210 ms. Participants were asked to shift their gaze from the fixation cross to the saccade target as soon as the saccade target appeared on the screen. At the onset of a head-moving block, participants were told that they were free to move their head while shifting their gaze but they should start each trial with their head oriented about 30° to the left of the fixation cross.

To be able to present the bar near the moment of the saccade, we predicted the saccade onset for each new trial on the basis of the average saccadic latency (the time between the presentation of the saccade target and the start of the saccade) on previous trials (Maij et al., 2009). The bar was presented for one frame near the predicted time of the saccade onset (about 140 ± 50 ms [M , SD] after the presentation of the saccade target), at one of the five possible locations. The saccade target was still visible at the time of the presentation of the green bar.

The participants were asked to touch the screen with the index finger of their dominant hand at the location at which they saw the bar. By the time they touched the screen all stimuli had disappeared. If participants did not see the bar for some reason, they could indicate having missed it by touching the bottom of the screen. Once the screen had been touched, a new trial started with a new fixation cross appearing at a new position on the screen.

Data analysis

Eye and touch position

The EyeLink's head-referenced eye-position data for the right eye were combined with the estimated head movement to yield a gaze movement. The gaze-movement data were used to determine characteristics of the primary saccades (the first saccades after the saccade target appeared on the screen). The first of two consecutive sampling intervals for which the tangential velocity of the gaze movement exceeded $35^\circ/s$ was considered to be the saccade onset, and the first

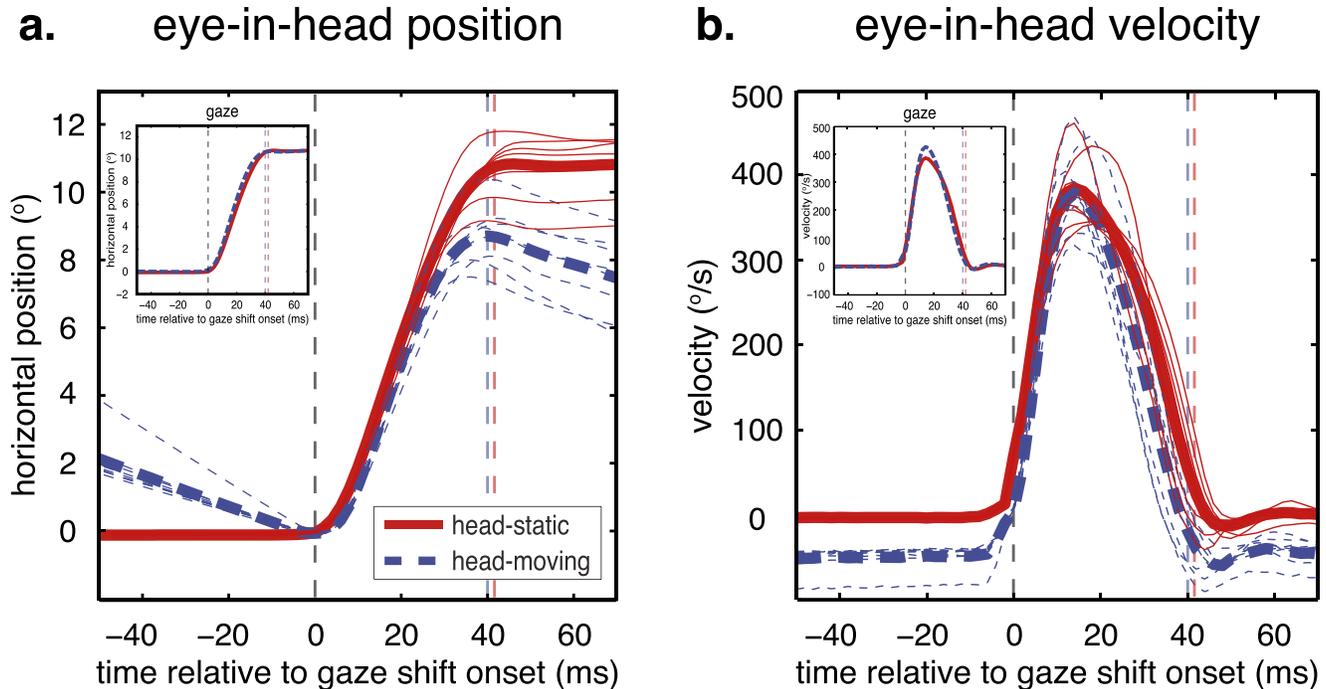


Figure 2. Characteristics of the saccades: (a) Eye-in-head position. (b) Eye-in-head velocity. The thick solid red curve shows the average eye orientation near the time of the saccade in the head-static trials and the thick dashed blue curve shows the average eye orientation near the time of the saccade in the head-moving trials. The thin red and blue curves show the individual participants' data. The vertical dashed black line shows the gaze-shift onset, and the dashed red and blue lines the average gaze-shift end in the head-static and head-moving trials, respectively. The insets show the gaze position and velocity in the same format as we show the eye-in-head position and velocity.

subsequent sample at which the velocity returned below this value was considered to be the saccade endpoint. We tested whether the movement of the head had an effect on the kinematics of the gaze or the eye using paired t tests on amplitude, duration, and peak velocity (Figure 2).

The first position at which the finger touched the screen was considered to be the perceived position of the bar; if the bottom of the screen was touched, that was taken as an indication that the participant had not seen the bar.

Trials were discarded if there was no saccade between 100 ms before and 100 ms after the time of the presentation of the bar (wrong timing; about 11.5% of the head-static trials and about 22% of the head-moving trials); if the length of the saccade was less than 50% or more than 150% of the 12° distance between the fixation cross and the saccade target (wrong amplitude; about 2% of the head-static trials and about 3% of the head-moving trials); if the direction of the saccade deviated by more than 22.5° from a movement to the right (wrong direction; about 1% of each kind of trial); if the saccadic reaction time was less than 75 ms or more than 300 ms (wrong latency; about 5.5% of the head-static trials and about 7.5% of the head-moving trials); or if the touched location differed by more than 12° in the direction of the saccade or by more than 3° perpendicular to the direction of the saccade from the actual location of the

bar (wrong or no localization—mainly trials in which participants touched the bottom of the screen to indicate that they had not seen the bar; about 6% of the head-static trials and about 5.5% of the head-moving trials).

Mislocalization pattern

We were mainly interested in localization in the horizontal direction (the direction of the saccade). We therefore defined the perceived position of the flashed bar as the horizontal distance from the fixation cross to the touched location. As the saccade latency varied from trial to trial, the bar was presented at various times relative to saccade onset. To draw a smooth curve through the mislocalization data as a function of the timing of the flash, we determined the mislocalization at each instant by averaging the perceived positions before and after that instant with weights based on a moving Gaussian window ($\sigma = 7$ ms) for each of the 10 conditions (five bar locations; head static or moving). We considered only times for which there were at least five data points within $\pm\sigma$. We refer to the resulting curves as mislocalization curves. We determined the mislocalization curves for each participant and condition and then averaged the values at each moment for each condition across participants (Figure 3).

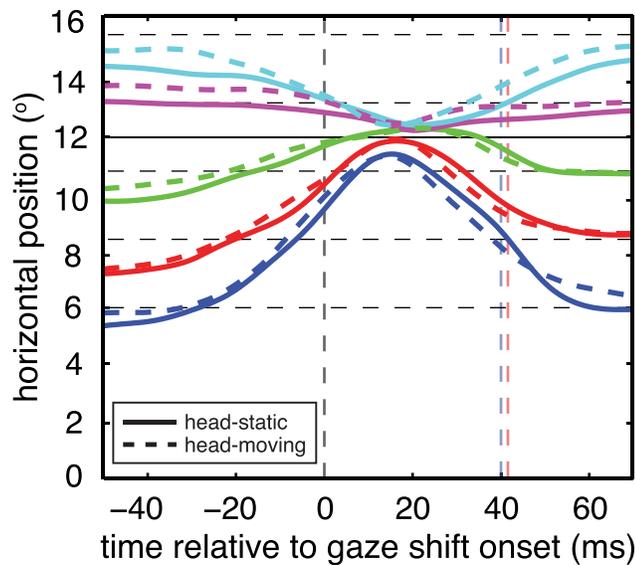


Figure 3. Average mislocalization with the head static and the head moving. The bar locations are indicated by horizontal dashed black lines. Each curve is a smoothed average of the perceived locations of green bars presented at various times relative to saccade onset. Each of the curves was first determined for each participant, and then the curves were averaged. The instruction was to make saccades from the black fixation cross (0°) to the black saccade target (solid black line at 12°). The vertical dashed black line shows the gaze-shift onset, and the vertical dashed red and blue lines the average gaze-shift end when the head was static and when the head moved, respectively.

To determine a single value for the amount of compression at each time of the flash relative to gaze-shift onset, both when the head was static and when the head moved, we took the values of the mislocalization curves (i.e., the average perceived positions) at the time in question for each flash location and plotted them as a function of flash position (example shown as an inset at the upper right of Figure 4). We fit lines through the values for the five flash positions, both when the head was static and when the head moved, and defined compression as 1 minus the slope of the fitted line (Maij et al., 2011b). We tested whether the kind of trial had an effect on the mislocalization pattern at each moment with paired t tests.

Results

Eye movements

In the head-static blocks, 11,967 of the 16,200 trials (about 74%) resulted in useful localization judgments; the number of trials in which participants indicated

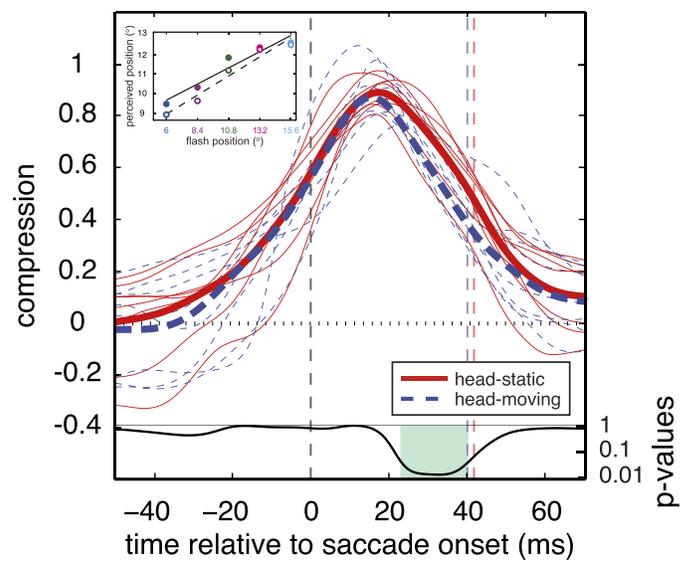


Figure 4. Average compression with the head static and the head moving. The thick solid red curve shows the average compression when the head was static, and the thick dashed blue curve shows the average compression when the head moved. The thin red and blue curves show the individual participants' data for each condition. The inset at the upper left shows an example of how the compression was determined for each time (35 ms after gaze-shift onset in this example). It shows the value of the mislocalization curve for each flash location when the head was static and when it was moving, at the time in question, with the best linear fit to these values. Compression is defined as 1 minus the slope of this fit. The vertical dashed black line shows the gaze-shift onset, and the vertical dashed red and blue lines the average gaze-shift end when the head was static and when the head moved, respectively. The inset at the bottom shows the p value for the difference between the two conditions for the whole time range. The green shaded area indicates where the p value is below 0.05.

that they had not seen the green bar was 954 (about 6% of the trials). The first saccades in the trials that resulted in useful localization were characterized by a mean reaction time of 127 ms, a mean eye-in-head (and gaze) amplitude of 10.7° , and a duration of 42 ms.

In the head-moving blocks, 12,515 of the 20,600 trials (about 61%) resulted in useful localization judgments; the number of trials in which participants indicated that they had not seen the green bar was 1,139 (about 5.5% of the trials). The first saccades in the trials that resulted in useful localization were characterized by a mean reaction time of 116 ms, a mean eye-in-head amplitude of 8.7° , a gaze amplitude of 10.6° , and a duration of 40 ms.

The average time courses of the changes in eye orientation and velocity with respect to the head during the gaze shifts are shown in Figure 2 for both the head-moving and head-static trials. The eye-in-head ampli-

tude of the first saccades was about 2° smaller in the head-moving trials, $t(7) = 12.076$, $p < 0.001$. The amplitude of the gaze shifts was not significantly different, $t(7) = 1.894$. In the head-moving trials, the head velocity during the saccade was about $40^\circ/\text{s}$. By having trials start with the head oriented 30° to the left, we managed to ensure that the head started moving well before the saccade, and thus moved at considerable speed during the whole saccade. The peak eye-in-head velocity was independent of the head movement, $t(7) = 0.123$, so the peak gaze velocity was about $40^\circ/\text{s}$ higher in the head-moving trials (see inset in Figure 2b), $t(7) = 4.076$, $p < 0.005$. Consequently, the gaze shift was completed in 2 ms less in the head-moving trials, $t(7) = 7.638$, $p < 0.001$.

Mislocalization pattern

For both conditions, the pattern of mislocalization (Figure 3) is similar to the one found in previous studies, with a compression of perceived positions during the saccade and peaks in the mislocalization that occur slightly earlier in the saccade for flashes that are closer to the fixation cross than for ones that are further away in the direction of the saccade target (Awater & Lappe, 2004, 2006; Lappe et al., 2000; Majj et al., 2011a, 2011b; Matziridi et al., 2013; Ostendorf et al., 2007). There is also a systematic mislocalization (a bias in the direction opposite to that of the saccade) well before and after the saccade (Awater & Lappe, 2004; Lappe et al., 2000; Majj et al., 2011a, 2011b; Matziridi et al., 2013).

As can be seen in Figure 3, there were some systematic differences in the mislocalization patterns between the conditions. Unrelated to our predictions, flashes well before and after the saccade were mislocalized less when the head was moving. To be able to quantitatively test our prediction of reduced compression during the saccade when the head was moving during the gaze shift, we estimated the average amount of compression at each time of the flash relative to the gaze onset, both for the head-static and the head-moving trials (Figure 4). There was significantly less compression when the head moved than when the head was static for times between 23 and 40 ms after gaze-shift onset ($p < 0.05$). Peak compression was about 0.9 for both kinds of trials, $t(7) = 0.256$.

Discussion

When a flash is presented around the time of a saccade, it tends to be judged to have been closer to where the saccade ended than it really was. This

perisaccadic compression has been found to depend on saccade parameters such as amplitude (Lavergne et al., 2010) and peak velocity (Ostendorf et al., 2007). What was not yet clear was whether the relevant parameters were those of the gaze shift or of the rotation of the eye relative to the head. In most previous studies on perisaccadic mislocalization, the changes in gaze were fully generated by rotating the eyes in the stationary head, so this distinction could not be made. By comparing perisaccadic mislocalization with and without a contribution of head movement to the gaze shift, we could make the distinction between gaze and eye-in-head movements.

When looking at the time course of compression, we found no effect of head movement on the compression during the first half of the saccade, but significantly less compression 23 to 40 ms after gaze-shift onset when the head moved. The time course of the reduction in compression when both the eyes and head moved corresponded with the time course of the reduction in the eyes' velocities when both the eyes and head moved (compare Figures 2b and 4) rather than with the change in gaze velocity (inset of Figure 2b). Apparently it is the velocity of the eyes, rather than that of the gaze, that underlies the reported correlation between perisaccadic compression and the velocity (Ostendorf et al., 2007) and amplitude (Lavergne et al., 2010) of saccades.

Richard et al. (2011) also compared compression for large gaze shifts with and without head shifts. Compression was almost complete in all their conditions, with a tendency for moving the head to increase rather than decrease compression. The difference between their study and ours may be due to differences between the amplitudes of the gaze shifts (40° in their study; 12° in ours) or to the fact that the head started moving before the eyes in our experiment, whereas it appears to have started moving at the same time as (or even later than) the eyes in their experiment. Uncertainty about whether and how fast the head was moving at the time of the saccade might have increased the compression when the head contributed to the gaze shift in that study. We asked our subjects to start their head movement before the saccade, so that the head velocity did not change substantially near the time of the saccade.

It has recently been proposed that a combination of uncertainty about when exactly flashes occurred with respect to changes in the direction of gaze and a tendency to believe that flashes occurred near where one was looking is responsible for the compression of apparent positions of flashes presented around the time of saccades (Majj et al., 2011a; Matziridi et al., 2014). According to this reasoning, faster gaze shifts lead to stronger compression because the same temporal uncertainty corresponds with a larger spatial uncertainty for a faster change in gaze. If so, there will be less

compression when part of the gaze shift is performed by moving one's head, assuming that estimates of eye and head orientation at the time of the flash are independent, because the combined uncertainty about eye and head orientation at the time of a flash in a combined eye–head gaze shift will be smaller than the uncertainty about the eye orientation when the eyes shift gaze on their own. If we assume that the uncertainty about the orientation at the time of the flash is proportional to the speed of rotation, and that the proportion is similar for rotation of the eyes and head, then if 20% of the gaze shift is produced by rotating the head (and 80% by rotating the eyes in the head), the uncertainty will be reduced to $\sqrt{20^2 + 80^2} = 82\%$ of the uncertainty obtained by moving the eyes alone to achieve the same change in gaze. Small deviations from these assumptions would not change the fact that the uncertainty is dominated by the variation in eye-in-head movement. Our finding that eye-in-head velocity rather than gaze velocity is critical with respect to the resulting compression is therefore in line with this explanation of the compression component of perisaccadic mislocalization.

Other explanations for the compression of the apparent positions of flashes presented near the time of saccades do not directly explain our results, although they can undoubtedly be modified to do so. Explanations of compression based on remapping (Burr, Ross, Binda, & Morrone, 2010; Cicchini, Anobile, & Burr, 2014) do not explicitly make predictions about how moving the head as well as the eyes in order to shift one's gaze will influence the compression, but—assuming that the remapping is to a head-centric representation—it would make sense for eye-in-head movements to be critical, as we found. Explanations of compression based on purely visual factors (Atsma, Majj, Cornelil, & Medendorp, 2014; Zimmermann, Fink, & Cavanagh, 2013; Zimmermann, Morrone, & Burr, 2014) would predict that how gaze is shifted is irrelevant, which does not seem to be the case.

Keywords: eye movements, saccades, spatial vision

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