Vision Research 51 (2011) 154–159

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Peri-saccadic mislocalization is not influenced by the predictability of the saccade target location

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ARTICLE INFO

Article history:
Received 22 January 2010
Received in revised form 14 October 2010

Keywords:
Saccade
Mislocalization
Human
Uncertainty

ABSTRACT

Flashes presented around the time of a saccade are often mislocalized. The precise pattern of mislocalization is influenced by many factors. Here we study one such factor: the predictability of the saccade target's location. The experiment examines two conditions. In the first the subject makes the same horizontal rightward saccade to the same target location over and over again. In the second the subject makes saccades to a target that is jumping in unpredictable radial directions. A dot is flashed in the vicinity of the saccade target near the time of saccade onset. Subjects are asked to localize the flash by touching its location on the screen. Although various saccade parameters differed, the errors that subjects made were very similar in both conditions. We conclude that the pattern of mislocalization does not depend on the predictability of the location of the saccade target.

1. Introduction

We make more than hundred thousand saccadic eye movements every day. Across each saccade both the eye orientation and the retinal image change, so the brain needs to somehow integrate these changes into reliable estimates of relevant objects' locations. This integration is prone to errors when brief stimuli are presented around the time of a saccade (e.g. Bischof & Kramer, 1968; Lappe, Awater, & Krekelberg, 2000; Maij, Brenner, & Smeets, 2009; Matin & Pearce, 1965; Pola, 2004; Ross, Morrone, & Burr, 1997; Schlag & Schlag-Rey, 2002). Such peri-saccadic mislocalization has been studied intensively and it has been shown to depend on many factors. For instance, the presence of visual references (Dassonville, Schlag, & Schlag-Rey, 1995; Honda, 1993; Lappe et al., 2000; Maij, Brenner, Chul-Li, Cornelissen, & Smeets, 2010), stimulus luminance (Georg, Hamker, & Lappe, 2008), stimulus contrast (Michels & Lappe, 2004), auditory information about the time of the flash (Maij et al., 2009) and saccade speed (Ostendorf, Fischer, Finke, & Ploner, 2007) have all been shown to modify the pattern of peri-saccadic mislocalization.

In daily life, we make saccades in various directions in rapid succession, in response to the content of the scene and in accordance with our intentions (Yarbus, 1967). In contrast, most studies of peri-saccadic mislocalization constrain the saccades in order to reduce the variability between trials (e.g. Lappe et al., 2000; Morrone, Ross, & Burr, 2005). In those studies, subjects are instructed to fixate a dot at a fixed position on the screen. When the dot disappears the subject has to make a horizontal saccade towards a second dot, the saccade target, which is always at the same place.

We examine whether subjects localize peri-saccadic flashes differently when the saccade target is always at the same position on the screen than when the position of the saccade target is unpredictable. A reason for expecting a difference is that when the subject is following a dot that is jumping in random directions on the screen, the goals of the saccades are not known until the target jumps. When the saccade target is always at the same position on the screen, the location of the saccade target and the initial orientation of the eyes are known well in advance. Several saccade parameters (such as latency and amplitude) are related to the predictability of the location of the saccade target (de Grave & Bruno, 2010). Moreover, Xu-Wilson, Zee, and Shadmehr (2009) showed that peak velocity of saccades to targets that contain information is higher than that to targets without information. Peak velocity has been shown to be positively correlated with the compression of the perceived flash locations towards the saccade target (Ostendorf et al., 2007). As predictable targets contain less meaningful information than unpredictable targets, we predict that unpredictable targets will give rise to faster saccades with more compression.

2. Methods

2.1. Design and subjects

We conducted the experiment in a normally illuminated room. Five subjects volunteered to participate in the experiment

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doi:10.1016/j.visres.2010.10.024

(including one of the authors). All subjects had normal or corrected-to-normal vision. The study is part of a research program that was approved by the ethics committee of the Faculty of Human Movement Sciences.

2.2. Experimental setup

Visual stimuli were presented on a touch screen (EloTouch CRT 19″, 1024 × 768 pixels, 36 × 27 cm, subtending a visual angle of 40° × 30°, 85 Hz) using the Psychophysics Toolbox in MATLAB (Brainard, 1997). The visual stimuli were viewed from a distance of 50 cm. Eye movements were registered using an Eyelink II (SR Research Ltd., Mississauga, Ontario, Canada) at a sample frequency of 500 Hz using the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002).

2.3. Stimuli and conditions

We used two conditions that differed in the saccades that the subjects needed to make (Fig. 1). One condition contained saccades in random directions and the other condition contained only rightward horizontal saccades. In the random direction condition, subjects were asked to follow a 0.5° diameter jumping white dot (108 cd/m^2) with their eyes. The dot was presented at a new position every 400 ms. It jumped in steps of 11° across a gray screen (100 cd/m^2), and remained on the screen until the next dot appeared. The white dot jumped in series of 3, 4 or 5 steps (random with equal probabilities). Each jump displaced the dot in one of eight radial direction, chosen at random from the two horizontal, two vertical and four diagonal directions, but never choosing a direction that would bring the dot within 4.7° (115 pixels) from the edge of the screen. In the rightward condition there were only two possible positions of the white dot; the saccade start and the target location were respectively 5.5° to the left and right of the screen centre. The white dot at the saccade start location was presented for 400 ms, before jumping to the saccade target location.

Shortly after the white dot was presented at its final position, a 0.5° diameter black dot (7 cd/m^2) was flashed (one frame) at one of 5 different locations with respect to the displacement between the (last) two positions of the white dot. The flashes were presented at 25%, 50%, 75%, 125% and 150% of the (last) displacement of the white dot (with 0% being its location before the displacement and 100% its location after the displacement). The saccade target was removed one frame before the flash. The trial ended when the subject indicated where he or she had perceived the flash by touching the screen. The next trial started after a random delay. Each subject took part in several sessions, and the two conditions were presented in different orders in different sessions.

2.4. Calibration

Before each session the subject was asked to calibrate the touch screen using the standard nine-point calibration provided by EloTouch, and to calibrate the Eyelink II using the standard nine-point calibration procedure of the Eyelink II.

To synchronize the eye movement recordings with the images presented on the screen, we always presented a second flash at the same time as the flash that the subject had to localize. The second flash was only used to synchronize the eye movement recordings with the images presented on the screen. It was presented in the lower right corner of the screen and was invisible to the subject. We measured the moment of this second flash with a photo-diode that was attached to the screen. The photo-diode sent a signal to the parallel port of the Eyelink computer. This signal was registered in the data file on the Eyelink computer. The temporal relationship between such a record and the record of the eye orientation at the moment of the flash was previously determined by using the photo-diode to drive an infrared lamp that 'blinded' one of the Eyelink cameras. Because the photo-diode was placed in the lower right corner, and the flash was presented at different locations on the screen, the real timing was only known to within a few milliseconds (we did not correct for the temporal effects of variation in the position of the flash on the screen). For trials in which no signal was sent from the photo-diode to the parallel port (24% of all trials; due to technical failure), we used the average delay between the record of the command to show the flash (that was also recorded on the Eyelink computer) and the record of the signal from the photo-diode (when such a signal was recorded) to estimate when the flash had occurred. On average, this delay was 27 ms, with a standard deviation of 3.5 ms. The latter is about what one would expect for variability within one frame of the image. Thus the accuracy of the timing was only slightly poorer on trials in which there was no signal from the photo-diode.

To estimate the errors that arise from using pointing as a response we also tested the accuracy of touching the location of a dot that remains present on the screen. The dot appeared at random positions and had the same size and color as the flash in the experiment. The average lateral and vertical standard deviation when localizing such dots is 0.25°.

2.5. Procedure

Because the mislocalization of the flash only occurs around the moment of the saccade, we wanted to present as many flashes as possible at about that time. We used the saccadic latencies on previous trials in the same direction to predict the saccade onset (Maij et al., 2009). We used the average saccadic latency on the ten

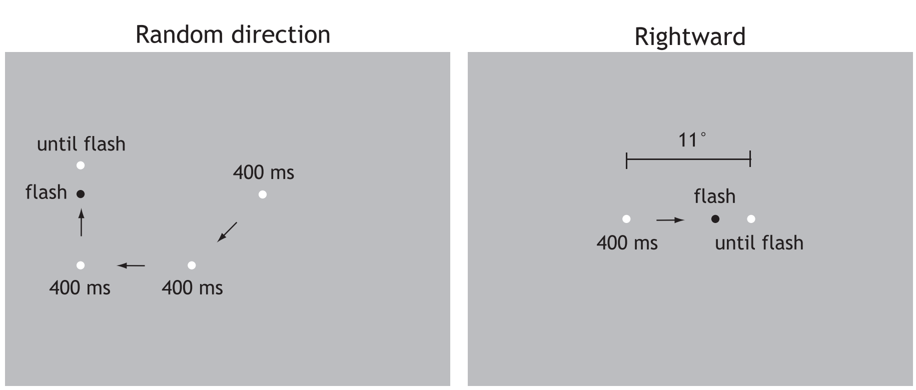

Fig. 1. Schematic overview of target positions for a single trial of each condition. Left panel: white dots jumped in random directions on the screen. A black dot was flashed near the saccade target shortly after the white dot's last jump. Right panel: the white dot jumped rightwards between two fixed locations. The black dot was flashed shortly after the second white dot appeared on the screen. All positions are shown in this overview, but there was never more than one target on the screen.

previous trials in which the saccades were in the same direction as that of the trial in question for the prediction. We used Dafoe, Armstrong, and Munoz (2007) average latencies for each direction at the beginning of each session. At the predicted saccadic latency the black dot was flashed on the screen for one frame at 25%, 50%, 75%, 125% or 150% of the last displacement of the white dot.

The subjects were asked to touch the screen as accurately as possible at the location at which they saw the black flash. If no new white dots appeared and the subject had not seen a black flash (for instance because he or she blinked when the flash was presented), the subject could indicate having missed the target by touching the screen in one of the corners. The trial ended when the subject touched the screen. In total there were 300 trials in each block and two blocks in each session (one for each condition). Subjects performed at least four sessions. If, after several sessions, there were too few successful trials for one of the conditions or directions, additional sessions were performed for that condition (the definition of a successful trial will be explained in the next section).

2.6. Data analysis

We used the *Eyelink's gaze position data* for the right eye to determine characteristics of the saccades, and the first location at which the finger touched the screen as the perceived position. For an eye movement to be considered to be a saccade, its tangential velocity had to exceed 35°/s for at least two consecutive samples (4 ms). The saccade end was at the first sample at which the tangential velocity was below 10°/s. We discarded trials in which there was no saccade near the time of the flash (*wrong flash timing*; see Fig. 3). We also discarded trials if the length of the saccade was less than 75% of the (last) displacement of the white dot (*wrong amplitude*) or if the direction of the saccade was not within ±22.5° of the radial direction of the (last) displacement of the white dot (*wrong direction*). Furthermore, we discarded trials in which the touched location differed by more than 270 pixels (11°; a whole displacement of the white dot) in the direction of the saccade, or 135 pixels (5.5°) perpendicular to the direction of the saccade, from the actual location of the flash (*wrong localization*). Doing so removes trials in which the subject touched one of the corners.

We only analyzed the localization in the direction in which the saccade target jumped: the component of the vector between the touched location and the true location of the flash in the direction of the (last) displacement of the dot. We plotted the true and perceived positions of the flash, relative to the (last) displacement of the white dot, as a function of the different moments of the flash, relative to saccade onset. To draw a smooth curve through the data (for each condition and flash position) we averaged the perceived positions for each subject and condition with weights based on a (moving) Gaussian window (σ = 7 ms). The smooth curve was drawn as long as there were at least 5 data points within 7 ms of the peak of the Gaussian. We will refer to this curve as the mislocalization curve.

2.7. Compression and shift

To describe the mislocalization in terms of compression and shift, we took the values of individual subjects' mislocalization curves at a single time sample (a horizontal position in Fig. 2A), plotted them as a function of flash location, and fit a line through these values (Fig. 2B). Compression was defined as 1 − arctan(θ), where θ is the angle between the fitted line and a horizontal line. In this definition, a compression of 0 means no compression, in contrast with other definitions of compression (e.g. Lappe et al., 2000). Shift was defined as the value of the fitted line for a (hypothetical) flash at the saccade target (flash position = 11°). Compression and shift were calculated separately for each time sample (Fig. 2C and D).

2.8. Maximum compression

To relate the compression to various other parameters we determined the maximal compression for each subject. The difference in maximum compression between the random direction saccade condition and the rightward saccade condition was tested with a paired *t*-test. We also determined the correlation of several saccadic parameters (amplitude, direction, peak velocity, standard deviation in peak velocity, latency and standard deviation in latency) with the maximum compression.

3. Results

On average, subjects did 4856 ± 729 trials for the random direction condition, and 2474 ± 783 trials for the rightward condition (mean ± standard error of the mean). The larger number for the

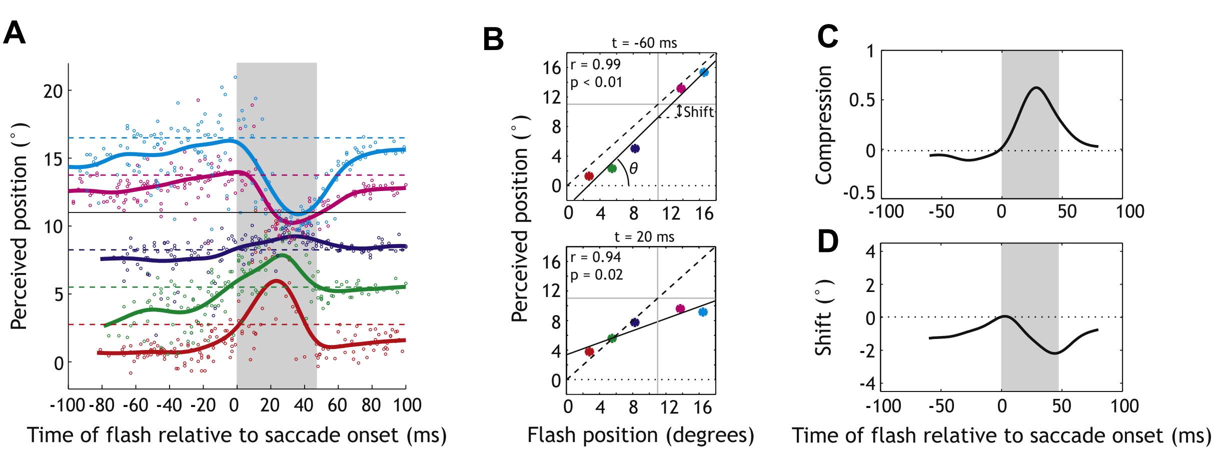

Fig. 2. Data analysis (data of one naïve subject for the rightward saccade condition). Gray bar: average saccade duration. Solid grey line: saccade target location. (A) For each flash location (dashed lines), the perceived positions for individual flashes (dots) were smoothed to obtain mislocalization curves. (B) Each dot shows the value of the mislocalization curve for one flash location at a certain time of the flash (at −60 ms in the top panel and 20 ms in the lower panel). Dashed line: veridical percept. Black line: best linear fit. We define compression as 1 − arctan(θ), so that a value of 1 is total compression and a value of 0 is no compression. Shift is defined as the value of the best linear fit at the saccade target location. (C) Compression for each time sample. (D) Shift for each time sample.

former was obtained by running additional sessions with only the random direction condition. In Fig. 3 we show the proportion of successful trials (the trials that were used in the further analysis) and the reasons why trials had to be discarded.

The saccadic latencies were significantly more variable for the saccades of the rightward condition than for those of the random condition (averaged across all directions; Fig. 4B; $p < 0.01$). The average saccade amplitude did not differ significantly between the two conditions (Fig. 4C). The saccade duration was significantly larger for the random direction condition (Fig. 4D; $p < 0.05$). As expected, the peak velocity of the saccades in the random direction condition was significantly larger than for the rightward saccade condition (Fig. 4E; $p < 0.05$) and the peak velocity was also significantly more variable (Fig. 4F; $p < 0.05$).

We also compared the saccade parameters of the rightward saccades of the random direction condition with those of the rightward condition. The average saccadic latency was significantly larger and the variability in latency was significantly smaller for the rightward saccades in the random direction condition than for those of the condition with only rightward saccades (Fig. 4A; $p < 0.05$ and $p < 0.01$, respectively). The peak velocity of the rightward saccades of the random direction condition was significantly larger than that of the condition with only rightward saccades (Fig. 4E, $p < 0.01$). In general, the rightward saccades were similar to all other saccades in the random condition.

Average mislocalization, compression and shift curves are shown in Fig. 5. The curves look very similar for both conditions. However, in particular before the saccade, there appears to be a difference in compression. Comparing the mislocalization patterns for saccade targets near the screen centre and near the border (random direction condition) showed that this effect is not related to the location of the saccade target on the screen (not shown). When only rightward saccade trials of the random direction condition were considered, we found a mislocalization pattern that was similar to the overall pattern for the random direction condition (see dashed curves in Fig. 5). Thus the direction of the saccades is also not responsible for the difference.

We tested whether there was a significant difference in the maximum compression between the two conditions. We did not find a significant difference ($p = 0.08$). Moreover, the maximum compression is not correlated with the mean peak velocity for either condition (Fig. 6; rightward condition: $r = 0.49$, $p = 0.40$, random direction condition: $r = -0.48$, $p = 0.41$). We also examined the correlation between maximum compression and the other saccadic parameters that we had determined (latency, standard deviation in latency, amplitude, duration and standard deviation in peak velocity) for both conditions. We only found a correlation between the maximum compression and the standard deviation in latency, and this was only significant for the rightward direction condition ($r = 0.97$, $p = 0.005$; not shown).

4. Discussion and conclusion

We found the predicted faster saccades for the random direction condition, but not the predicted associated increase in compression. We even found a slight reduction of compression. The difference in the compression was most evident for flashes presented well before the saccade, and gradually decreased during

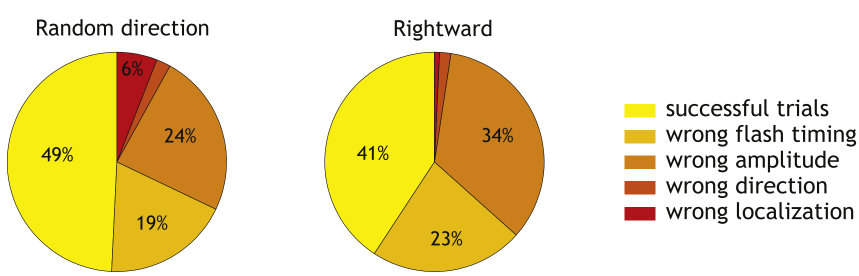

Fig. 3. Percentage of successful and discarded trials for each condition. If trials were unsuccessful on several criteria they were assigned to the first on the list. When the percentage is smaller than 3% the value is only shown graphically.

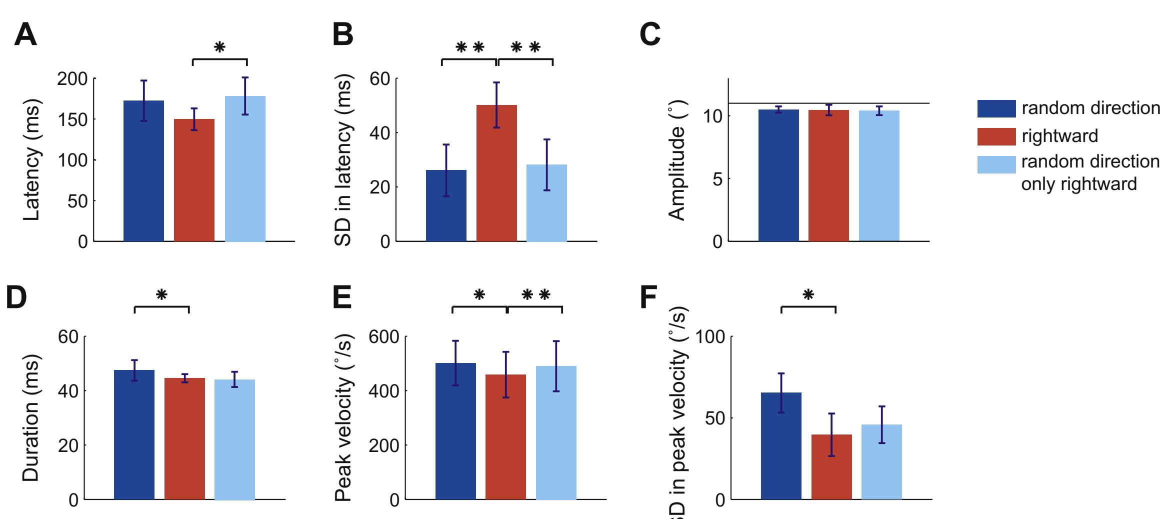

Fig. 4. Several parameters of the (last) saccades. All parameters were first determined per subject and subsequently averaged across subjects. Error bars show standard errors across subjects. (A) Saccadic latency. (B) Standard deviation in the saccadic latency. (C) Saccade amplitude. The gray horizontal line shows the amplitude of the target jump. (D) Saccade duration. (E) Peak velocity of the eye during the saccade. (F) Standard deviation of the peak velocity.

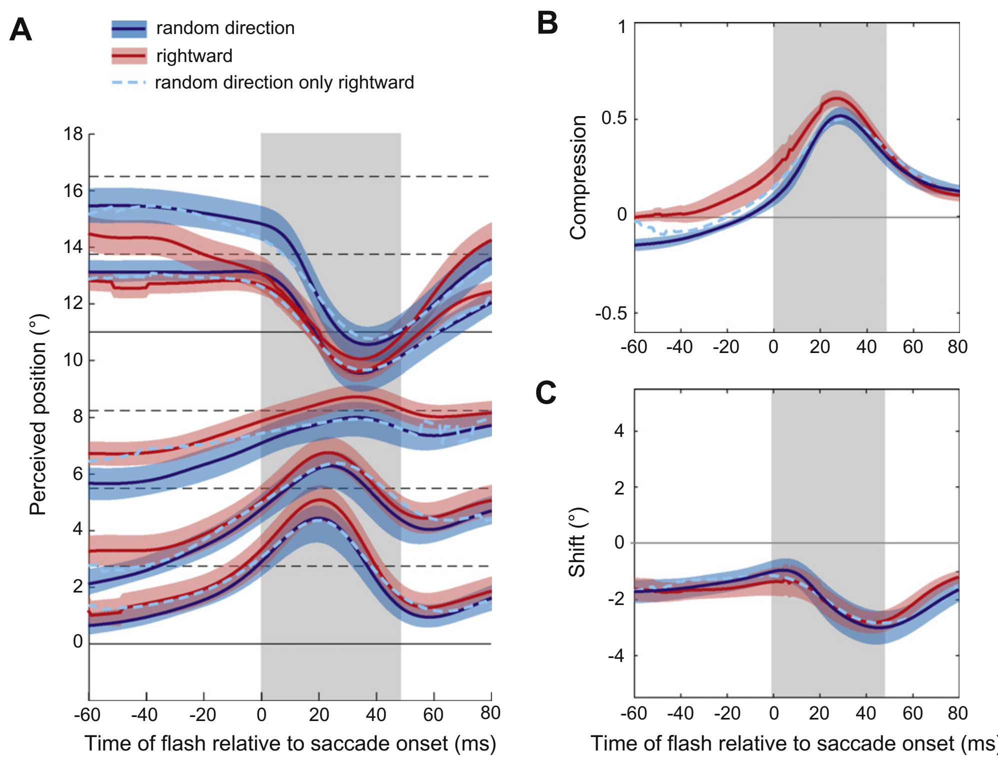

Fig. 5. Mislocalization (A), compression (B) and shift (C) curves averaged across the five subjects. The gray vertical bars show the saccade duration. The red and blue colored curves and the transparently colored areas show the average with standard error of the mean across subjects for the random and rightward condition. Cyan dashed curves: average mislocalization curves for only the rightward saccades of the random direction condition. Dashed horizontal lines: flash locations. Solid horizontal lines: saccade target locations and the initial fixation target for rightward saccades. The discontinuities that are visible in some of the averaged curves are due to missing data of a single subject. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

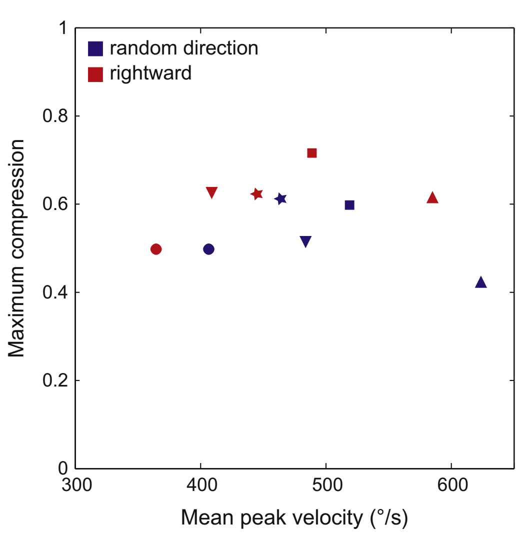

Fig. 6. Maximum compression versus mean saccadic peak velocity for the five subjects. Colors represent different conditions and symbols different subjects.

the saccade (see Fig. 5). In accordance with the departure from the prediction, we did not find the previously reported positive correlation (across subjects) between compression and mean peak velocity of the saccades, on which the prediction was based (see Fig. 6; Ostendorf et al., 2007). Thus it is unclear how we should interpret the small difference in compression that we do find.

We excluded two possible reasons for the found difference: the position on the screen and the directions of the saccades. Another possible source for the small difference in compression might be the variable start location of the saccade in the random direction condition. Subjects might use the remembered saccade start location as a reference for localizing the flash. In the rightward saccade condition the start location was always the same, so subjects are unlikely to misjudge it systematically (the appearance of the start location on each new trial provides feedback). With random locations the perceived location of the start of the saccade is more likely to be misjudged systematically (for instance always judging it to have been closer to where the flash had occurred). Systematically misjudging the saccade start location could change the perceived location of the flash if the flash is considered to have occurred before the saccade. Relying on the misjudged position of the saccade start location would explain why the small difference in compression that we found for flashes presented before the saccade gradually decreases during the saccade.

The method we use to determine compression and shift is different from the one that was introduced by Lappe et al. (2000). They defined the shift index based on the mean of the perceived flash locations, and the compression index on the standard deviation of the perceived flash locations. Both their indices are normalized to their respective average values 100 ms before and after the saccade. One disadvantage of this method is that the flash locations must be arranged symmetrically around the saccade target location. Otherwise, a pure compression towards the saccade target will be interpreted as being accompanied by a shift, because the compression is not towards the average flash location. Also, the normalization to the average value 100 ms before and after the saccade is rather arbitrary, and would transform any compression or shift for flashes before (or after) the saccade to an apparent effect at other moments. The definition that we used is more flexible in this respect, but is not fundamentally different.

Another methodological point is that making saccades to follow a dot as it jumps in random directions is a very natural thing to do. It is similar to what we do in daily life; we respond to the content of the scene and the task at hand by making saccades in various directions in rapid succession. When instructed to only make rightward saccades, we found that subjects have shorter saccadic latencies and the latencies of the saccades are more variable (Fig. 4). This made it harder to present the flashes around the time of the saccade (so we had to discard more trials for the rightward condition, as shown in Fig. 3). Subjects sometimes even did not make any saccade at all in the rightward condition (in Fig. 3 these are indicated in the category *wrong flash timing*). Thus the task was easier to perform when the subject needed to follow a dot jumping in random directions than when they always had to follow the same displacement of the dot.

To summarize, in this paper we show that the predictability of the saccade target does not influence the mislocalization pattern (although the predictability of the starting point of the saccade might). Flash positions are mislocalized systematically near the time of saccades, but the extent to which this occurs is largely independent of how long in advance the saccade can be anticipated.

Acknowledgments

We thank Siro Otten and Frans-Josef Halkes for their technical support. This research was supported by the Netherlands Organization for Scientific Research (NWO, ALW Grant 816-02-017).

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