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RESEARCH ARTICLE

Visual mislocalization during saccade sequences

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Abstract Visual objects briefly presented around the time of saccadic eye movements are perceived compressed towards the saccade target. Here, we investigated perisaccadic mislocalization with a double-step saccade paradigm, measuring localization of small probe dots briefly flashed at various times around the sequence of the two saccades. At onset of the first saccade, probe dots were mislocalized towards the first and, to a lesser extent, also towards the second saccade target. However, there was very little mislocalization at the onset of the second saccade. When we increased the presentation duration of the saccade targets prior to onset of the saccade sequence, perisaccadic mislocalization did occur at the onset of the second saccade.

Keywords Saccade · Compression of visual space · Double-step paradigm

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Introduction

Saccade eye movements shift the eyes in a ballistic fashion, causing frequent rapid shifts of the retinal image, posing the problem of how vision remains stable across eye movements (for a recent review see Melcher and Colby 2008). Saccades cause drastic changes in visual perception: stimuli flashed briefly around the time of saccades are mislocalized, seen displaced in the direction of the saccade, and compressed towards the saccade target (Ross et al. 1997, 2001; Morrone et al. 1997; Lappe et al. 2000; Hamker et al. 2008; Lavergne et al. 2012; Zirnsak et al. 2014). Cicchini et al. (2013) showed that for pairs of bar-stimuli, one presented perisaccadically, the other before or after, the perisaccadic stimulus was mislocalized towards the stimulus presented during pre- or post-saccadic fixation. These experiments led the authors to conclude that saccadic compression may be related to the mechanisms attempting to match objects seen before saccades with those seen after. When there is only one stimulus, flashed briefly just before saccade initiation, the system attempts to pair it with a visual salient stimulus seen after fixation, with similar shape and dynamics. We have recently shown that compression critically depends on the visual saccade target signal (Zimmermann et al. 2014a). When we asked subjects to perform saccades onto a blank, screen compression was reduced strongly. The visual saccade target signal does not have to be physically present, a representation of it held in memory is sufficient to induce compression.

Here, we asked about the role of the visual target signal in saccade sequences. A classical method for studying sequences is the double-step paradigm, in which two targets are presented in brief succession and extinguished before execution of the first saccade (Westheimer 1954; Hallett and Lightstone 1976). Planning and execution of

the second saccade in the double-step paradigm therefore has to rely on a memory representation of the saccade target signal. Since the first saccade dissociates the retinal target location from its position in external space coordinates, the spatial position of the target held in memory must be updated after performance of the first saccade. We measured perisaccadic mislocalization at the time of the first and the second saccade in the double-step paradigm. This allowed us to ask whether perisaccadic mislocalization can be observed with an updated target signal.

How does the oculomotor system re-calculate the position of the second saccade target position after execution of the first saccade? It has been suggested that the second saccade target position can be estimated by a vector subtraction mechanism based on the retinotopic representation (Goldberg and Bruce 1990). Evidence for saccade sequence coding comes from studies which show that saccade parameters like latency and duration change with the length of the saccade sequence (Zingale and Kowler 1987). Saccade sequence planning is further supported by an inverse relationship between the latency of the first saccade, and the intersaccadic interval between the two (Becker and Juergens 1979; McPeek et al. 2000). Others proposed an updating of the second saccade target position around the time of the first saccade: temporary disruption of the pathway from the superior colliculus via the mediodorsal thalamus to the frontal eye fields disables the updating process and consequently saccades land at a location corresponding to the remembered retinal position and not the actual position of the second saccade target (Sommer and Wurtz 2002). Behavioral evidence consistent with the idea of updating showed that errors of the first saccades were compensated by the second saccade (Joiner et al. 2010; Collins 2010). However, there is also evidence that saccade target position can be coded in a spatiotopic format which is independent of gaze direction: saccades are made accurately to memorized targets despite intervening saccades induced by electrical stimulation in the superior colliculus (Mays and Sparks 1980).

In this study, we measure spatial localization of stimuli displayed near the onset of the first or second saccade. We find surprisingly little mislocalization of stimuli displayed around the onset of the second saccade. However, when the saccadic target was displayed for a long duration before the saccade sequence commenced, there was strong mislocalization during both saccades. We suggest that for mislocalization to occur, the position of the saccadic target needs to be encoded robustly, and this takes time.

Materials and methods

Subjects were seated 57 cm from a 22″ CRT colour monitor (Barco Calibrator: 120 Hz, 800 × 600 pixels) with head stabilized by chin- and headrest, viewing binocularly the 40 × 30° visible field. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), which samples gaze positions with a frequency of 2,000 Hz. The system detected start and end of a saccade when eye velocity exceeded or fell below 22°/s and acceleration was above or below 4,000°/s^2. Before each session, the system was calibrated with the eyelink 9-point calibration. Each calibration was checked with the eyelink validation procedure. In all experiments, the background was red (7 cd/m^2) and the fixation points and saccade targets were black (0.5 cd/m^2). All experiments were carried out in a dimly lit room.

Experiment 1

Subjects fixated a fixation point for variable duration of 1,000–1,500 ms. The fixation point was then switched off, and the first saccade target appeared for 60 ms (Fig. 1). The fixation point and the saccade targets were presented in all trials at: FP: −15°/14° T1: −15°/−1° T2: 0°/−1° as a black rectangle (0.75° × 0.75°, 18.6 cd/m^2). With offset of the first saccade target, the second saccade target was shown 15° to the right of the first saccade target for 60 ms (unless otherwise stated). Subjects were instructed to initiate the saccade sequence as soon as the first target appeared. Since the saccade reaction time was around 160 ms both saccadic targets disappeared before the first saccade starts. A probe dot (diameter: 0.75°, green: 18.6 cd/m^2) was presented for 8 ms at a time randomly chosen between saccade target onset and second saccade landing. The probe dot was shown pseudo-randomly in one out of 8 possible locations (11.25°/−1°, −11.25°/−1°, 17.5°/−1°, −7.5°/−12.25°, 11.25°/10.25°, −7.5°/10.25°, −15°/10.25°, −15°/−12.25°). The mouse cursor appeared

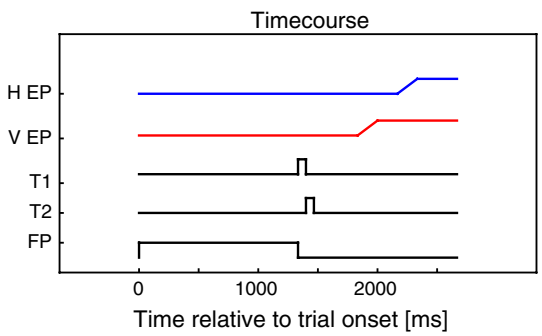

Fig. 1 Timecourse of events of the double-step task. The fixation point is shown for a variable time between 1,300 and 1,500 ms. With offset of the fixation point, the first saccade target (*T1*) appears for 60 ms. Simultaneously, with the disappearance of target *T1,* saccade target *T2* was presented for 60 ms. The subject performed first a vertical then a horizontal saccade

1000 ms after the offset of the second saccade target, which the subject used to indicate the apparent position of the probe dot. Clicking the left screen corner indicated that the subject had not detected the probe dot during a trial (discarded from analysis).

Experiment 2

In Experiment 2, all parameters of the set-up were the same as in Experiment 1, except that saccade target T2 now was displayed 300 ms after the offset of saccade target T1. This way the second saccade target was no longer shown before the onset of the first saccade, and saccade sequence planning was disabled.

Experiment 3

In Experiment 3, the positions of the fixation point and the saccade targets were the same as in Experiments 1 and 2. However, the presentation duration of the two saccade targets were systematically varied. After a fixation period of 1,000–1,500 ms, the targets were shown for either 60 or 500 ms. The fixation point remained visible for this additional duration until the targets were extinguished. The offset of the fixation point was to go-signal for the subject to perform the two saccades to the remembered target positions.

Participants

Three subjects (one author, two naive subjects, mean age = 29 years) participated in all experiments, over several testing days. In the first experiment, we collected in total 7,928 trials, in the second 32,449 trials, in the third 31,896 trials, and in the fourth 3,510 trials. All subjects had normal or corrected-to-normal vision. Subjects gave informed consent. The experiments were carried out along the principles laid down in the declaration of Helsinki.

Results

Experiment 1

Three observers judged the position of probe dots briefly flashed (for 8 ms) while they performed a double-step saccade sequence. Two saccade targets were shown, the second immediately following the first, each for 60 ms (Fig. 1). Subjects initiated the two saccade sequence as soon as the target for the first saccade appeared, so neither target was presented during either saccade (Fig. 1). The first saccade was a vertical saccade and subjects undershot the saccade target by 2.37° (SD: 2.13°) on average. The second saccade was in horizontal direction, and saccades landed on the saccade target on average were precisely (SD: 2.33°). Average saccade latency was 160 ms for the first saccade and 368 ms for the second saccade. Latencies are calculated by subtracting the time of saccade onsets from the onset time of the first saccade target. The average intersaccade interval, i.e. the duration between end of the first and start of the second saccade, lasted 150 ms.

Figure 2 shows mislocalization of probe dots presented around the time of the first or second saccade. Plots are aligned to the onset of either the first (Fig. 2a–c) or second (Fig. 2d–f) saccade. Each data point represents one measurement from a single trial for one observer: results of all three observers are pooled. Lines represent running means, continuously averaging over 20 trials. The first saccade was downwards, which may be expected to produce vertical compression towards the T1 at onset of the first saccade. This is what occurred. Around onset of the first saccade, all probe dots parallel to the saccade path were mislocalized in the direction of the saccade target (Fig. 2b). Some mislocalization orthogonal to the saccade path was also observed (Fig. 2a), particularly for the more eccentric positions (as previously reported Kaiser and Lappe 2004), but far less than in the vertical direction. Figure 2c shows the mislocalization during the perisaccadic period (20 ms before saccadic onset) as vectors: the length and direction of each arrow indicates mislocalization, with the base showing baseline localization (long before execution of the saccade), and the arrowhead the average apparent position during for perisaccadic presentations. All arrows near the saccade path point to the first saccade target, indicating a clear pattern of compression, primarily in the vertical direction. For stimuli on the right part of the screen (hence more peripheral), there was also a horizontal component to the compression.

The second saccade in the double-step sequence was horizontal, which may be expected to produce horizontal compression at saccadic onset. However, as can be seen in Fig. 2d, there was very little mislocalization at the onset of this saccade. Probe dots in all locations were perceived close to their veridical position, which is also obvious from inspection of the vector lengths of Fig. 2f. This result shows that a briefly flashed visual saccade target signal has to be presented retinotopically matched to the future saccade landing position to induce compression.

We calculated 2 × 8 ANOVAs with the factors "saccade number (first or second)" and "Probe position" separately for the horizontal and the vertical localization component. For the horizontal component, the significant main effect "saccade number" ($df = 1$, $F = 54.682$, $p < 0.000$) confirmed stronger mislocalization for the first than the second saccade. The significant main effect "Probe position" ($df = 7$, $F = 47.451$, $p < 0.000$) and the significant

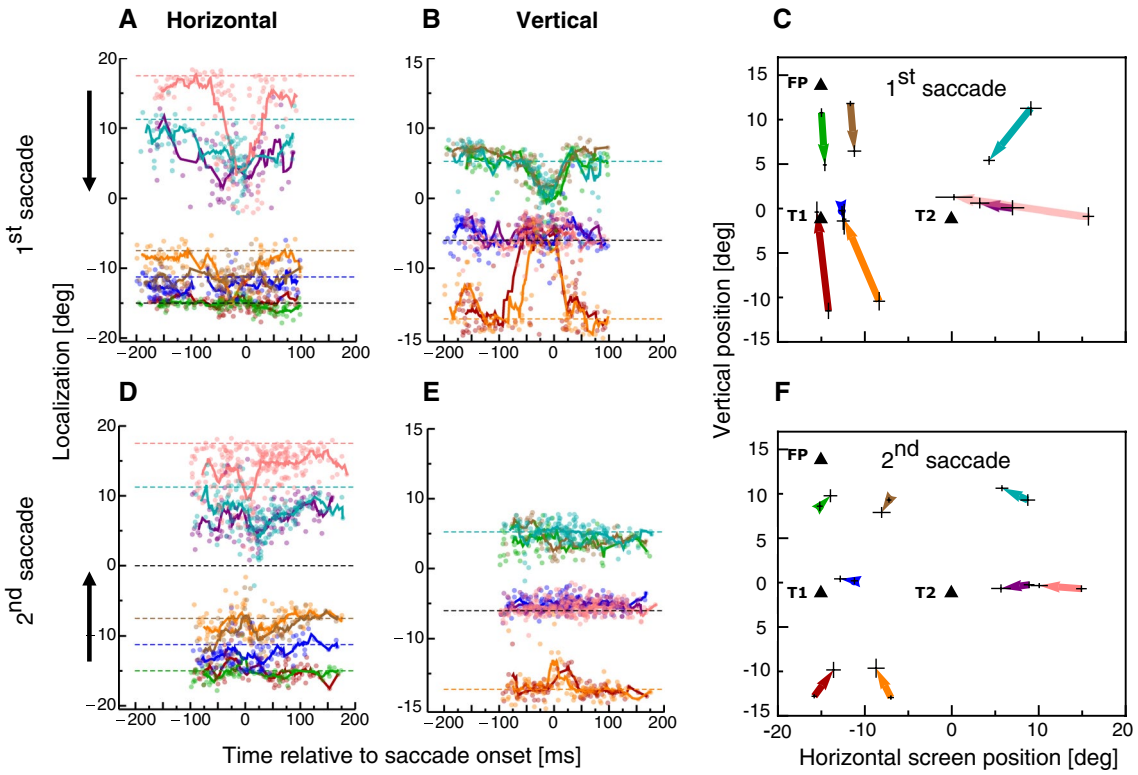

Fig. 2 **a** Horizontal localization of the probe dot as a function of time relative to onset of the first saccade in the double-step task. *Different colours* refer to the eight different positions of the probe dot as shown in (**c**). The thick curves report binned data averaged across subjects and trials, and single dots report single trials from all subjects. **b** Vertical localization of the probe dot: otherwise like **a**. **c** Mislocalization of probe dots at onset of first saccade. The start of each *arrow* represents baseline localization from 100 ms before onset of the first saccade. The *arrowhead* indicates peak mislocalization at first saccade onset. *Error bars* indicate the horizontal and vertical SEM of the baseline and the peak mislocalization. **d** Horizontal localization of the probe dot relative to onset of the second saccade. Same conventions as **a**. **e** Vertical localization of the probe dot relative to onset of the second saccade. Same conventions as **a**. **f** Spatial distribution of mislocalization at second saccade onset. Same conventions as **c**

interaction effect ($df = 7$, $F = 6.081$, $p < 0.000$) showed that the mislocalization parallel to the saccade path was stronger than the orthogonal one. Similarly, for the vertical component both factors, "saccade number" ($df = 1$, $F = 155.818$, $p < 0.000$) and "Probe position" ($df = 7$, $F = 712.173$, $p < 0.000$) as well as the interaction ($df = 7$, $F = 274.339$, $p < 0.000$) were significant.

Experiment 2

In order to confirm the idea that briefly flashed targets have to be shown in the retinotopic-matched position to induce perisaccadic compression, we modified the double-step task so that the second saccade target was presented after the first saccade had been executed. In this situation, the saccade target was presented such that it matched the retinotopic position of the saccadic goal. The first saccade was a vertical saccade and subjects undershot the saccade target by 1.89° (SD: 2.28°) on average. The second saccade was horizontal and undershot the target on average by 1.75° (SD: 2.08°). Average saccade latency was 161 ms for the first saccade and 350 ms for the second saccade. The average intersaccade interval lasted 220 ms.

The mislocalization results with this paradigm (Fig. 3) show that under these conditions perisaccadic compression is mostly parallel to the saccade path, for both the first and the second saccade. The vertical compression at onset of the first saccade was very similar to that of the double-step sequence, but in this condition, there was no horizontal mislocalization for peripheral dots. At the onset of the second saccade, there was strong horizontal mislocalization towards the second target, much the same as occurs with single saccades.

We have shown earlier that spatiotopic representations take time to construct (Zimmermann et al. 2013a, b; Zimmermann et al. 2014b). We therefore studied the effect of time to build up by systematically varying the time of presentation of the second saccade target. In these trials, both saccade targets were presented for 60 ms, but the second target was displayed 300 ms after the offset of the first.

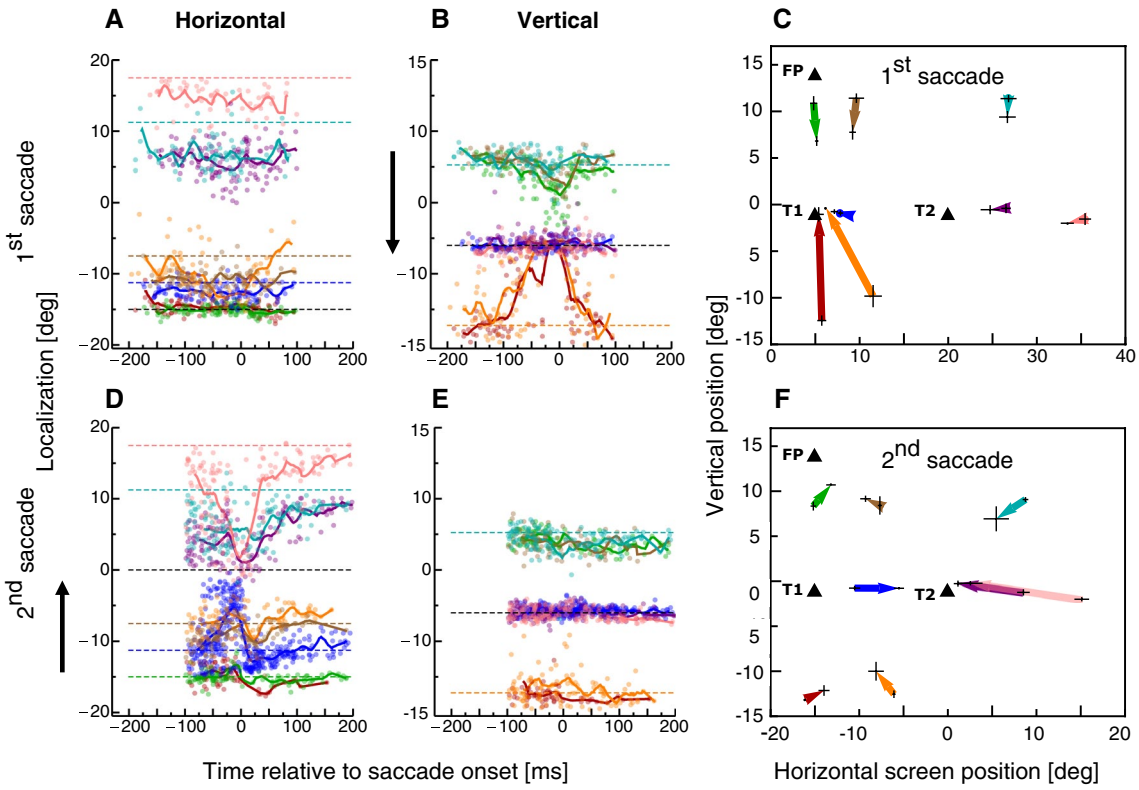

Fig. 3 **a** Horizontal localization of the probe dot relative to onset of the first saccade. *Different colours* refer to the eight different positions of the probe dot as shown in Fig. 1c. The two panels report *horizontal* and *vertical* localizations respectively. **b** Vertical localization of the probe dot relative to onset of the first saccade. Same conventions as **a**. **c** Mislocalization of probe dots at onset of first saccade. The start of each *arrow* represents baseline localization from 100 ms before onset of the first saccade and the *arrowhead* peak mislocalization at first saccade onset. Data were averaged across subjects and trials. *Error bars* indicate the horizontal and vertical SEM of the baseline and the peak mislocalization. **d** Localization of the probe dot relative to onset of the second saccade. Same conventions as **a**. **e** Spatial distribution of mislocalization at second saccade onset. Same conventions as **b**

The time of presentation of T2 relative to the onset of the first saccade was calculated on a trial-by-trial basis, and binned into four latency bins (depending on both delay of target presentation and saccadic latency). For each bin, we measured the magnitude of compression, which we define as the slope of the linear regression of the perceived against physical position: zero corresponds to complete compression, one to veridicality). The amount of compression at the time of the second saccade clearly increased with the time of T2 relative to onset of the first saccade. Figure 4 plots the compression index as a function of time of T2 (relative to the onset of the first saccade). When the second T2 appeared before or within 50 ms of the onset of the first saccade, there was little compression. However, when T2 was displayed 150 ms or more after the onset of the first saccade, compression was strong.

Mislocalization magnitude for each probe dot position was defined by the difference in localization of probe dots presented in the perisaccadic range (±25 ms around saccade onset) from the average baseline localization (dots presented 100 before initiation of the first saccade).

We calculated 2 × 8 ANOVAs with the factors "saccade number (first or second)" and "Probe position" separately for the horizontal and the vertical localization component. For the horizontal component, the main effect "saccade number" was not significant ($df = 1$, $F = 0.376$, $p < 0.541$), indicating that in this task, compression was statistically indistinguishable between the two saccades. The significant main effect "Probe position" ($df = 7$, $F = 28.057$, $p < 0.001$) and the significant interaction effect ($df = 7$, $F = 22.742$, $p < 0.000$) showed that the mislocalization parallel to the saccade path was stronger than the orthogonal one. Similarly, for the vertical component, the factor "saccade number" was not significant ($df = 1$, $F = 0.431$, $p < 0.513$), while the main effect "Probe position" ($df = 7$, $F = 275.171$, $p < 0.001$) and the interaction ($df = 7$, $F = 225.180$, $p < 0.000$) were significant.

We calculated bootstrapped t tests between the binned presentation time of target T2 before onset of the first saccade (leftmost data point in Fig. 4) and the three bins with presentation times after onset of the first saccade. When the second saccade target T2 was presented only 50 ms after

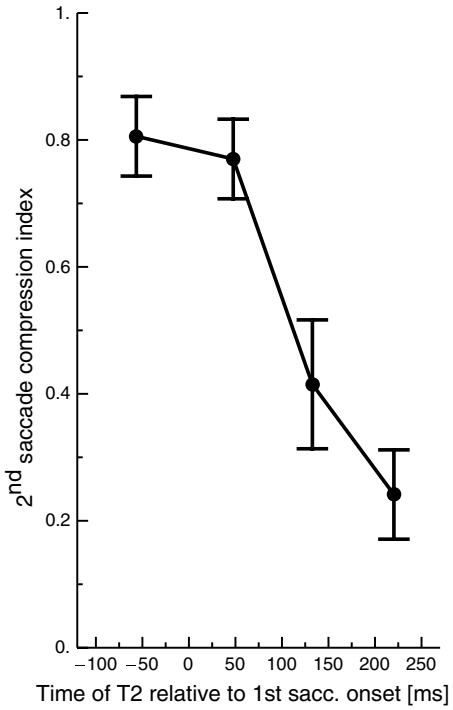

Fig. 4 Compression magnitude at onset of second saccade as a function of the timing of the second saccade target T2, relative to first saccade onset. The size of the *horizontal bars* indicates the bin width. *Vertical bars* are SD of the compression magnitude derived by bootstrapping

first saccade onset, no significant difference in mislocalization was found ($p = 0.27$). However, for the later presentation time of 125 ms or at 225 ms, significant differences were observed ($p < 0.01$ inboth cases).

Experiment 3

The previous experiment shows that the amount of compression of the second saccade depends directly on the time between the two saccades. Is this because a pause is required between saccades? Or does the system require time to encode the location of T2 robustly, so it becomes an anchor for compression? To test these two possibilities, we repeated the study with T1 and T2 displayed for a variable amount of time *before* initiation of the two saccade sequence. The probe dot was shown pseudo-randomly in one out of 5 possible locations (−11.25°/4°, −7.5°/4°, 7.5°/4°, 11.25°/4°, 17.5°/4°). Subjects maintained fixation on the fixation point until it was extinguished, after extinction of T1 and T2. T1 was displayed either for 60 or 500 ms, followed immediately by T2 for the same duration (see Fig. 5a). Subjects saccaded to T1 when the fixation point (FP) was turned off. For the 60 ms target presentation duration, the first saccade target T1 was undershot by 0.43° (SD: 1.60°) and the second target T2 by 1.05° (SD: 4.05°). For the 500 ms target presentation duration, the first saccade target T1 was undershot by 0.45° (SD: 1.53°) and the second target T2 by 1.34° (SD: 3.24°).

Figure 5b shows how the magnitude of horizontal compression (at the onset of the second saccade) varies with exposure duration of T1 and T2. Compression increases significantly with the duration of the saccade targets (bootstrap t test, $p < 0.001$). Figure 5c, d shows localization of probe dots at second saccade onset for 60 and 500 ms presentations of T1 and T2. Localization was near veridical for brief target presentations, but for 500 ms, there was strong compression towards T2. These figures also illustrate the method of calculating the compression index, described above. The compression index was 0.8 ± 0.03 for the short presentation, 0.43 ± 0.04 for the long presentation (errors represent the standard deviations derived by bootstrapping data pooled across trials and subjects). These results suggest that the important parameter for compression is the time available for encoding the position of T2 at the time of execution of the first saccade. Note that our effects cannot be influenced by a possible retinal afterimage, as the targets are dark on a light background and the exposure is probably too short to generate a strong afterimage. Further, an afterimage would be located in retinotopic locations after the first saccade and therefore cannot account for compression found at the updated saccade target location around the time of the second saccade.

The intersaccadic interval, the time between the landing of the first and the initiation of the second saccade, changed considerably with increasing saccadic target presentation. When saccade targets were presented for only 60 ms, the intersaccadic interval was short with an average duration of 241 ms (Fig. 5e). However, increasing target exposure led to a longer mean intersaccadic interval of 280 ms (Fig. 5f).

Discussion

No mislocalization at onset of second saccade for briefly flashed targets

We investigated visual mislocalization with the double-step paradigm to examine whether the visual saccade target signal that drives perisaccadic mislocalization is stored in a retinotopic or a spatiotopic reference frame. Perisaccadic mislocalization depends on a visual saccade target signal (Zimmermann et al. 2014a). During execution of two saccades in the classical double-step paradigm where the targets are briefly flashed (60 ms), mislocalization is strong during performance of the first saccade. Stimuli in all positions were misperceived in the direction of both the first and the second saccade target position. However, almost no mislocalization occurred at the onset of the second saccade.

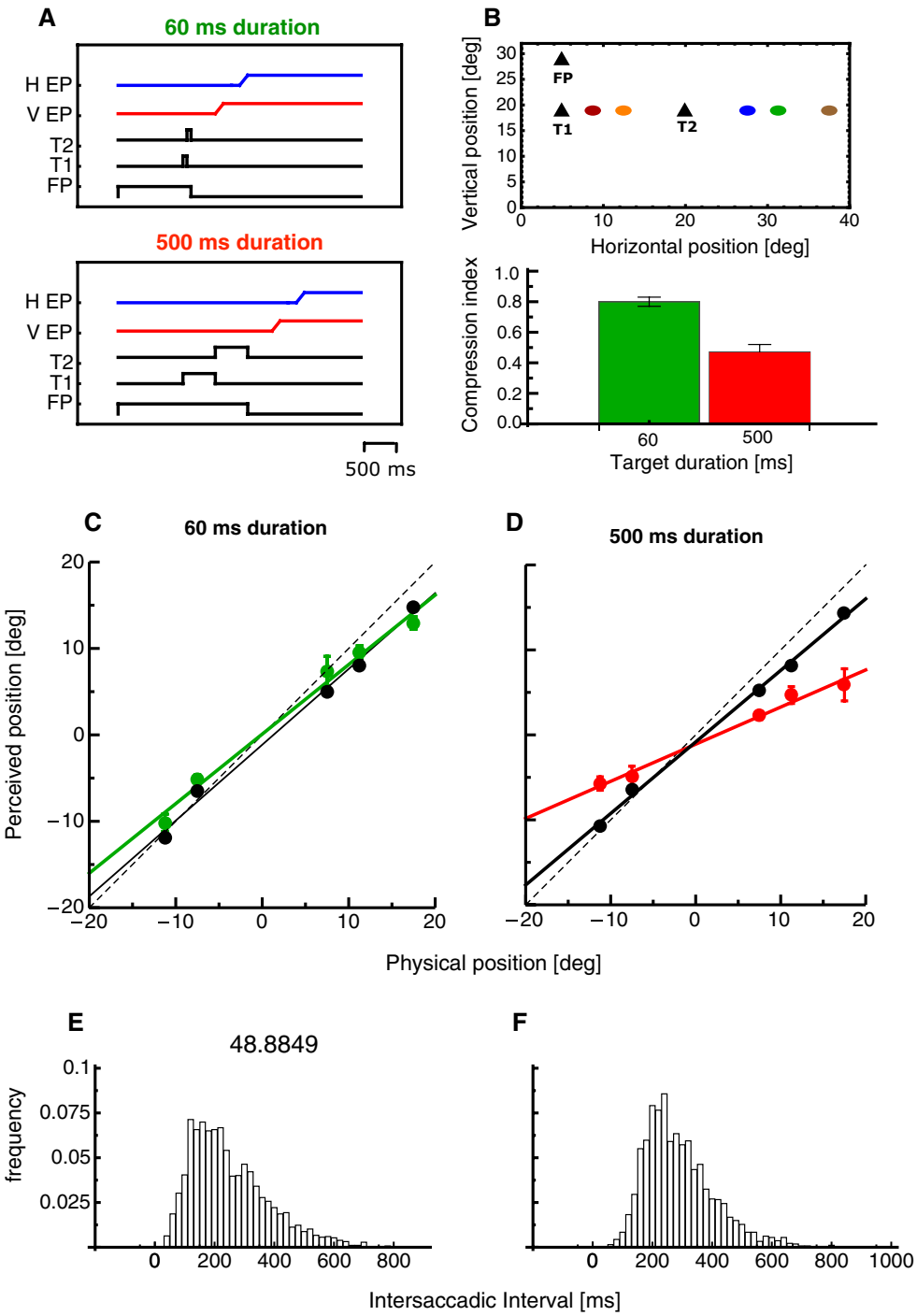

Fig. 5 **a** Timecourse of events in the double-step task where the saccade targets T1 and T2 were presented either for 60 ms (*upper panel*) or 500 ms (*lower panel*). **b** Average compression magnitude in trials with different presentation duration of the saccade targets T1 and T2 (between 60 and 500 ms). Data were averaged across subjects and trials. Errors are SE of the mean. **c** Results from the double-step task with 60 ms saccade target presentation. Physical position of the probe dot against perceived position for dots presented immediately at onset of the second saccade (shown in *green*) and for *dots* presented 500 ms after onset of the second saccade (shown in *red*). *Lines* represent the linear fit of the data (trials averaged across subjects), and *error bars* represent standard error. **d** Results from the double-step task with 500 ms saccade target presentation. Same conventions as **c**. **e** Duration of the intersaccadic interval for sessions in which the saccade targets were presented for 60 ms. The intersaccadic interval is defined as the duration from first saccade landing to the start of the second saccade. Data are binned with a bin width of 20 ms. **f** Duration of the intersaccadic interval for sessions in which the saccade targets were presented for 500 ms. The intersaccadic interval is defined as the duration from first saccade landing to the start of the second saccade. Data are binned with a bin width of 20 ms

Briefly flashed saccade targets thus have to be presented in a position retinotopically matched to the saccade goal to induce compression. The absence of mislocalization at the time of the second saccade is probably also influenced by the different retinal eccentricities of the second saccade target signal. When the target is shown before execution of the first saccade (as in "Experiment 1" section), the target is about 21° in the periphery. However, when the target is shown after execution of the first saccade (as in "Experiment 2" section), it is only 15° in the periphery. The higher eccentricity of the target in Experiment 1 might have further weakened its neural signal strength and thereby reduced perisaccadic mislocalization.

Earlier studies have suggested the importance of visual references for perisaccadic compression: first, studies conducted in complete darkness in the absence of any visual references reported a shift in the direction of the saccade, but no compression component against saccade

direction (eg Honda 1989; Dassonville et al. 1992; Schlag and Schlag-Rey 2002). Second, Lappe et al (2000) used a memory-guided saccade paradigm in complete darkness and systematically varied the presence of visual references. They reported that visual references presented after execution of the saccade-induced compression. In all other cases, they found the perisaccadic shift.

We have recently shown (Zimmermann et al. 2014a) that when saccades are made to general regions of space, without specific targets, there is very little compression. When target-like stimuli are displayed at the same time, the compression tends to be towards them. We have also shown (Cicchini et al. 2013) that when two stimuli are presented in succession, one at saccadic onset, the other before or after the saccade, the perisaccadic stimulus tends to be drawn towards the pre- or post-saccadic stimulus. All this is consistent with the idea that a large component of the compression is visually driven. The saccade sequence was kept constant across trials; thus, any changes in mislocalization could be the result of an overlearning of the spatial positions. However, this is unlikely since any learning would affect the two saccade target positions in the same way. But the absence of mislocalization is only found at the time of the second saccade. Additionally, expectations of the saccade target position do not affect perisaccadic mislocalization (Maij et al. 2011).

Spatiotopic mislocalization in the second saccade when targets are presented longer

The pattern of mislocalization at the time of the second saccade changed when the saccadic targets were displayed for a long period, more than 200 ms, before subjects were cued to saccade. Then there was strong—almost total—compression at the onset of the second saccade. These results suggest that for saccadic compression to occur towards a position that is spatiotopically but not retinotopically matched to the saccade goal, the location of the target needs to be well coded in visual memory.

We have shown recently that spatiotopic representations take time to construct (for review see Zimmermann et al. 2014b). Visual tilt adaptation is remapped across a saccade to its spatiotopic position if the saccade target is cued for at least 500 ms before execution of the saccade (Zimmermann et al. 2013a). Consistently, saccadic suppression of displacement (Bridgeman et al. 1975), the inability to perceive intrasaccadic shifts of the saccade target within a certain range, reduced drastically when the saccade target was previewed (Zimmermann et al. 2013b). Also spatiotopic saccade adaptation emerged only after the saccade target had been previewed (Zimmermann 2013). All these data support the idea that spatiotopic representations are not created instantly, but develop slowly over time. This suggestion implies that the classical reactive saccade paradigm, where the target appears suddenly, might not be suited well to study spatiotopic representations.

Awater et al. (2004) showed that in an anti-saccade paradigm where a saccade has to be performed into the opposite direction of the saccade target, compression centres on the saccade landing position and not on the visual target position. This finding seems to contradict our hypothesis that compression is the result of an attempt to match the probe to an anchor stimulus. The anti-saccade task can be solved either by inverting the motor vector in the opposite direction or by remapping the visual target signal to the new position. Evidence suggests that the anti-saccade task may cause an inversion of the visual vector (Sato and Schall 2003). In this view, the visual activity of the anchor stimulus would be remapped to the anti-position. The focus of compression then would be driven by the remapped anchor activity.

Evidence for pre-planning in double-step saccades

The double-step paradigm usually involves brief target presentations (Westheimer 1954; Hallett and Lightstone 1976), and the evidence suggests that both saccades are pre-planned in parallel before the eyes start to move (Becker and Juergens 1979; McPeek et al. 2000). On this view, the oculomotor system calculates both saccade vectors in retinotopic coordinates by vector subtraction, avoiding the necessity to store visual position information of the saccade targets over the course of the first saccade. Our data with brief saccade target presentations confirm the idea of pre-planning: in many trials, latencies of the second saccade were unusually short compared with single saccades (see Fig. 5e). When the saccade targets were presented for 60 ms, the mean latency of the second saccade was 241 ms. With more prolonged presentation of the saccadic target (500 ms), however, the average second saccade latency increased to 280 ms. We believe that for the long saccadic target presentation, the visual memory representation is strengthened and saccade programming relies on a visual representation of the targets. This would explain also why compression was found at the time of the second saccade for long, but not for brief, saccadic target presentations.

We assume that for brief saccade target presentations, the oculomotor system pre-plans both saccades in retinotopic coordinates and calculates the second saccade by vector-by-vector subtraction. With the longer target presentation, however, the system can rely on visual target information in spatiotopic coordinates and can plan the second saccade after the first is finished, at expense of reaction time. Neural activity corresponding to saccade sequence pre-planning has been found in the superior colliculus (Sparks and Mays 1983; McPeek and Keller 2002) and the frontal eye fields (Goldberg and Bruce 1990; Hu and Walker 2011).

Conclusions

The absence of mislocalization during the saccade in the double-step paradigm with briefly flashed target reinforces the claim that perisaccadic compression depends on the visual saccade target signal. Perisaccadic compression therefore might be the signature of a mechanism connecting objects across the transient visual gap produced by the saccade (Cicchini et al. 2013). The return of mislocalization during the second saccade when the targets for shown longer before execution of the first saccade is consistent with the idea that spatiotopic representations take time to construct.

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