

Temporal dynamics of remapping captured by peri-saccadic continuous motion

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Different attention and saccade control areas contribute to space constancy by remapping target activity onto their expected post-saccadic locations. To visualize this dynamic remapping, we used a technique developed by Honda (2006) where a probe moved vertically while participants made a saccade across the motion path. Observers do not report any large excursions of the trace at the time of the saccade that would correspond to the classical peri-saccadic mislocalization effect. Instead, they reported that the motion trace appeared to be broken into two separate segments with a shift of approximately one-fifth of the saccade amplitude representing an overcompensation of the expected retinal displacement caused by the saccade. To measure the timing of this break in the trace, we introduced a second, physical shift that was the same size but opposite in direction to the saccade-induced shift. The trace appeared continuous most frequently when the physical shift was introduced at the midpoint of the saccade, suggesting that the compensation is in place when the saccade lands. Moreover, this simple linear shift made the combined traces appear continuous and linear, with no curvature. In contrast, Honda (2006) had reported that the pre- and post-saccadic portion of the trace appeared aligned and that there was often a small, visible excursion of the trace at the time of the saccade. To compare our results more directly, we increased the contrast of our moving probe in a third experiment. Now some observers reported seeing a deviation in the motion path but the misalignment remained present. We conclude that the large deviations at the time of saccade are generally masked for a continuously moving target but that there is nevertheless a residual misalignment between pre- and post-saccadic coordinates of approximately 20% of the saccade amplitude that normally goes unnoticed.

Keywords: saccade, remapping, spatial vision, continuous motion

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Introduction

Our visual world remains stable despite continual retinal shifts caused by eye movements. With every saccade, the perceived locations assigned to points on the retina must be updated to maintain their correspondence with the objects in the world. Single cell studies (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990) have shown that just before a saccade, cells in several areas respond to stimuli that are outside their receptive fields but that will fall on them after the saccade. These authors noted that this “remapping,” might play a critical role in reassigning perceived locations and maintaining space constancy. Behavior-

ally, many authors have seen this remapping as the source of the mislocalizations of position reported for brief flashes presented within 100 ms of the saccade (Lappe, Awater, & Krekelberg, 2000; Matin & Pearce, 1965; Ross, Morrone, & Burr, 1997; see review of Schlag & Schlag-Rey, 2002). Nevertheless, one concern about these observations is that measurement relies on a delayed report of the remembered briefly flashed location. Several studies have used flickering probes (Hershberger, 1987; Sogo & Osaka, 2001; Watanabe, Noritake, Maeda, Tachi, & Nishida, 2005) to visualize any mislocalizations as relative displacements between successive flashes as they happen. For sequences of flashes triggered during the saccade, the flickering dot was seen as an array of points whose individual

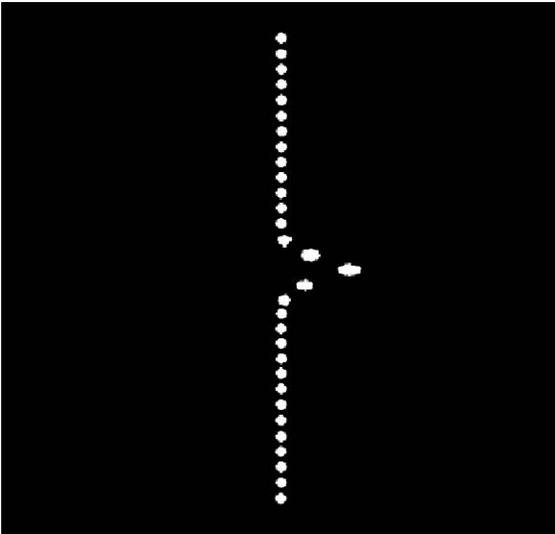


Figure 1. Schematic illustration of typical patterns of distorted trajectories observed in the 302 ms condition of Honda (2006) for a rightward saccade. The stimuli used was composed of 31 adjacent LEDs flashed in sequence, each for 2 ms with an inter-stimulus interval (ISI) of 8 ms. The resulting motion trajectory lasted 302 ms and traversed 18° vertically, lying midway between the fixation and saccade points that were themselves separated by 18° . Two observers reported seeing brief excursions as depicted here in one-third to one-half of the trials. The deviation lasted about 50 ms, going in the direction of the saccade, whereas the pre- and post-saccadic portions of the trace were always aligned (adapted from figure 2c of Honda, 2006).

locations corresponded to the mislocalizations seen for single flashes (Hershberger, 1987). However, if the flickering probe started flickering before the saccade, and specifically at the time of peri-saccadic mislocalization and compression, little or no mislocalization was reported, as if well-established position information overrode or stabilized any shifts that might have been seen for a single flash (Sogo & Osaka, 2001; Watanabe et al., 2005). The pre-existing position information appeared to outweigh any visualization of peri-saccadic mislocalization. Here we report a closely related perceptual measure, a moving probe, first used by Honda (2006), to determine if this probe will reveal peri-saccadic mislocalization as an easily seen, visual pattern.

Honda (2006) used a linear array of LEDs to present a moving probe and asked observers to make a saccade across this motion path. Following the saccade, observers drew the perceived motion trajectory. For very brief motion traces (38 ms and 52 ms) that overlapped with the saccade, the observers drew large curving mislocalizations in the apparent trace. According to Honda, these shifts were consistent with the estimates of mislocalization made from single flashes. However, if the motion probe had a longer duration

(302 ms) so that it started before and ended after the saccade, observers reported seeing a straight trace with the pre- and post-saccadic segments aligned, and occasionally with a small deviation away from and then back to the motion path at the time of the saccade (Figure 1). Honda's (2006) moving probe therefore did not appear to offer any further insight into mislocalization than the stationary probes of earlier experiments.

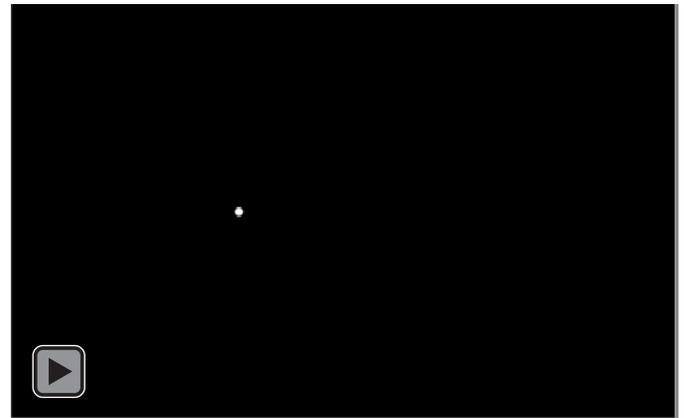
Nevertheless, we were interested in two aspects of the results from Honda's longer duration (302 ms) trace. First, when the excursion was seen (one-third of the trials for the first observer, and fewer than half of the trials for the second observer in Experiment 1), it was quite brief and small, as opposed to the properties that we would expect from the single flash experiments of peri-saccadic mislocalization and compression. In these experiments, brief flashes are mislocalized in a range of 150 ms to 200 ms around the saccade and have amplitude as large as the saccade itself (Lappe et al., 2000; Matin & Pearce, 1965; Ross et al., 1997; see review of Schlag & Schlag-Rey, 2002). Second, whether Honda's observers saw the excursion, they always drew the trace as aligned before and after the saccade. In contrast, our earlier study (Szinte & Cavanagh, 2011) found that the pre- and post-saccadic locations seen for a target in apparent motion across a saccade did not appear aligned. Instead, the results of that study suggested that in correcting for the shift of the saccade, the position of the pre-saccadic dot had been over-compensated by about 5%.

We see two reasons why Honda's results might differ from ours and from the earlier peri-saccadic mislocalization findings. First, Honda's report of an aligned trace before and after the saccade may have been a result of the continuous presence of the motion. The continuous trace provides a location reference for the probe position as the dot moves down the screen. Just as the pre-existing flicker probe suppresses temporary mislocalizations seen just before and after the saccade (Sogo & Osaka, 2001; Watanabe et al., 2005), the moving position reference may also suppress the trans-saccadic shift in coordinates (Szinte & Cavanagh, 2011) that remains uncorrected over larger time scales. Second, to capture the excursions in the motion trace, Honda's observers only made hand-drawn reports of their percept and so may have missed the misalignment and the large excursion away from and back to the vertical motion path at the time of the saccade. In other words, Honda's technique may have allowed a better visualization of mislocalization than the stationary flickering probes, but the deviation may have been too brief and/or dim to be reported in the hand-drawn measures of his participants.

To test the continuous motion stimulus more parametrically, we used a similar stimulus composed of a salient probe moving down the display before,

during and after saccade (Movie 1 and Figure 2a) that was fairly close in timing and configuration to the 302 ms condition of Honda's (2006) study (duration: 302 ms motion vs. 500 ms motion; configuration: 31 LEDs flashed successively at 10 ms intervals moving downward by 0.6° on each step for 18° of travel vs. 60 successive presentations of dot on a CRT at 8.33 ms intervals moving downward by 0.416° on each step to cover 25°). As in Honda's experiment, our probe's path was placed midway along and orthogonal to the saccade, so that the saccade produced a sharp lateral motion of the probe on the retina in the opposite direction of the saccade (Figure 2b).

To foreshadow our results, the moving probe when presented at low contrast was not seen to curve away from and then back toward its downward path; the pre-existing location information for the dot as it moved down the screen appeared to override any peri-saccadic mislocalization. Nevertheless, the trace appeared to be broken into two straight segments that did not line up, with the post-saccadic portion shifted in the saccade direction relative to the pre-saccadic portion (Figure 2e) consistent with our earlier result based on apparent motion (Szinte & Cavanagh, 2011). To measure the misalignment between the pre- and post-saccadic



Movie 1. Stimulus demonstration. Click on the video to make it start. Move your gaze to follow the jumping white dot. While moving your eyes, pay attention to the motion trajectory of the red square. The trajectory is best seen in a dark room on an otherwise dark monitor. Although the trajectory is straight, many observers (with uncontrolled display conditions) and all our participants in our experimental conditions, perceive two segments not one, with the earlier one seen offset horizontally from the second in the direction opposite to the saccade.

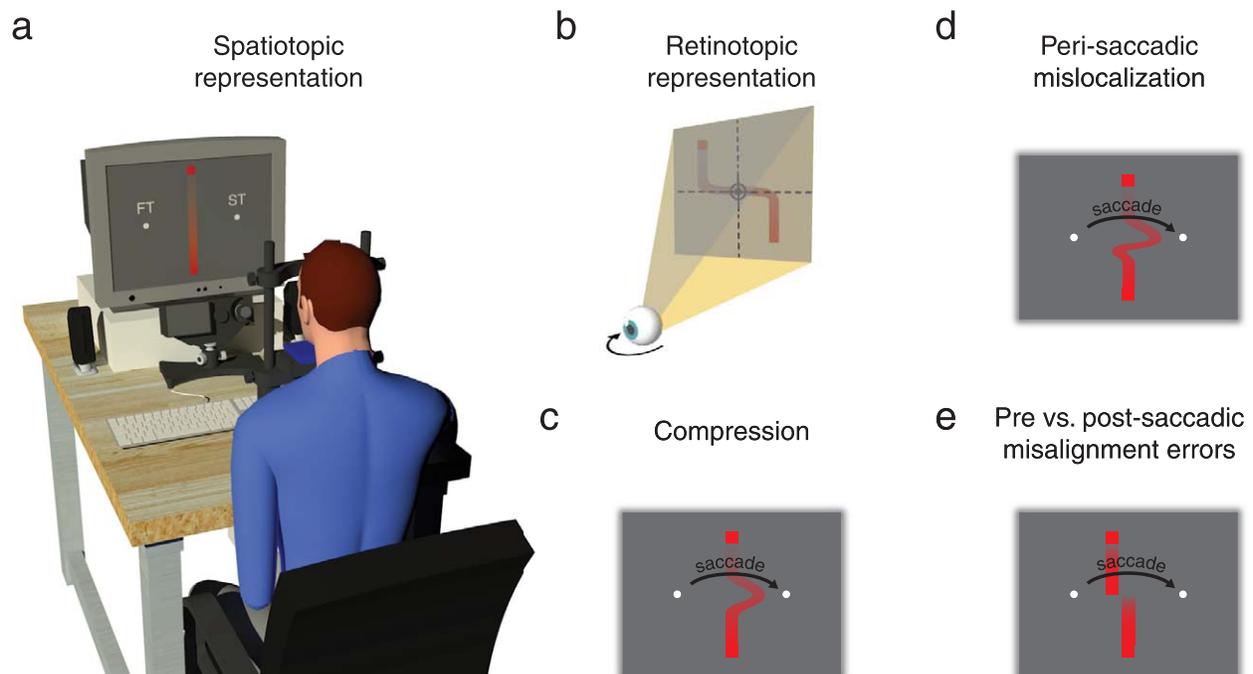


Figure 2. Visual representations. (a) Observers were instructed to saccade from a fixation target (FT) to a saccade target (ST) while a red square moved continuously downward. (b) On the retina, when observers performed a rightward saccade, the first part of the motion path falls to the right of the fovea while the second part falls to the left, crossing the fovea at the mid-point of the saccade. (c) From the prediction of the compression effect (Ross et al., 1997) the perceived motion should deviate toward the saccade target and then go back to the actual path just around the time of the saccade ("Compression"). (d) Peri-saccadic mislocalization literature will predict the same pre-saccadic effect but after the saccade the path should deviate toward the fixation target to then go back to the actual path. (e) Here, we observed that the motion appears as it is in space, with a systematic error of compensation leading to the perception of two motion traces that are horizontally misaligned ("pre vs. post-saccadic misalignment error").

segments, we introduced a blank in the central 200 ms bracketing the saccade. Then, to measure the timing of the break between the two segments, we presented the entire motion path with the appropriate counter-shift at different times relative to the saccade. This allowed us to evaluate the temporal dynamics of the shift by a simple report of motion continuity, and showed that the position compensation for the saccade occurred in time near the mid-point of the saccade itself. Finally, we increased the display contrast to be a better match to Honda's stimuli (2006), and found that the deviations around the time of the saccade became visible for some observers but the overall misalignment between pre- and post-saccadic segments remained as before.

Experiment 1

Materials and methods

Observers

Six volunteers from Université Paris Descartes took part in [Experiment 1](#) (one author, and five observers naïve to the purpose of the experiment, age 21–31 years, three males and three females). All had normal or corrected-to-normal vision and gave informed consent. The experiments were carried out according to ethical standards specified in the Declaration of Helsinki.

Instruments and stimuli

Observers were seated in a quiet, dimly lit room with their head positioned on a chin rest 60 cm in front of a computer screen. The fixation markers were 0.6°-diameter white dots (68.0 cd/m²) and the moving stimulus was a 1°-side red square (12.0 cd/m²), all on a dark-gray background (4.5 cd/m²), presented on a 22" Sony GMD-F520 screen (Sony, Tokyo, Japan) with a spatial resolution of 1,440 by 1,050 pixels (36.7° by 27.6°) and a vertical refresh rate of 120 Hz. The experiment was controlled by an Apple MacPro Dual Intel-Core Xeon computer (Apple, Inc., Cupertino, CA). The dominant eye's gaze position was recorded and available online using an EyeLink 1000 Desktop Mounted Eye Tracker (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 2 kHz. The experimental software controlling stimuli display and response collection was implemented in Matlab (MathWorks, Natick, MA), using the Psychophysics (Braunard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peter, & Palmer, 2002) toolboxes. Saccades were detected online when the gaze passed outside a virtual circle of 1.5°-radius centered on the fixation target and landed later within a second virtual circle of 2°-radius

centered on the saccade target. Eye movement data were also re-analyzed offline based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006) computed from subsequent samples in the eye position series. The thresholds for peak velocity and minimum duration used for saccade detection were 3 SD and 20 ms. Psychometric functions were fitted using the Psignifit toolbox (Wichmann & Hill, 2001a, 2001b).

Procedure

Each trial began with a fixation target made of a white circle, filled with a smaller, dark gray bull's-eye. This fixation target was presented on the horizontal midline of the screen and could appear 7.5° to the right or to the left of screen center leading to an equiprobable number of 15° rightward and leftward saccade trials. When the participant's gaze was detected within a 1.5°-radius virtual circle centered on the fixation target, the bull's-eye changed from dark gray to orange. The orange dot indicated that fixation was achieved and that the next trial would start momentarily. After 400 ms of correct fixation the target was entirely filled with white and the trial began. After a random period of fixation between 300 and 1100 ms (five possible times separated by 200 ms), a red square (the visual probe) appeared at 12.5° above the horizontal midline of the screen. This square always moved downward for 500 ms at a constant speed of 50°/sec, covering a vertical amplitude of 25° (stepping ~0.42° per screen refresh).

In the first experiment, the horizontal position of the moving probe varied between trials but started close to the screen midline. The central 200 ms segment of the probe's motion was blanked ([Figure 3a](#) and [Movie 2](#)), creating two motion segments of 150 ms each (7.5° amplitude each, blanked over the central 10°). This procedure gave the impression that the square passed behind an object of the same color as the background without changing its speed. In order to trigger a saccade during this blank period we presented the saccade target and simultaneously extinguished the fixation target 25 ms after the probe appearance. Observers were asked to saccade to the new fixation location and, all the while, to pay attention to the probe motion. Thus, after the appearance of the saccade target, the probe kept moving downward for another 125 ms and was blanked for 200 ms, and then reappeared for 150 ms. Finally, 200 ms after the end of the motion sequence a red ring appeared around the saccade target indicating that the observers should then report whether the second motion trace (the one after the probe blanking) was more to the left or to the right of the first motion trace (the one before the probe blanking).

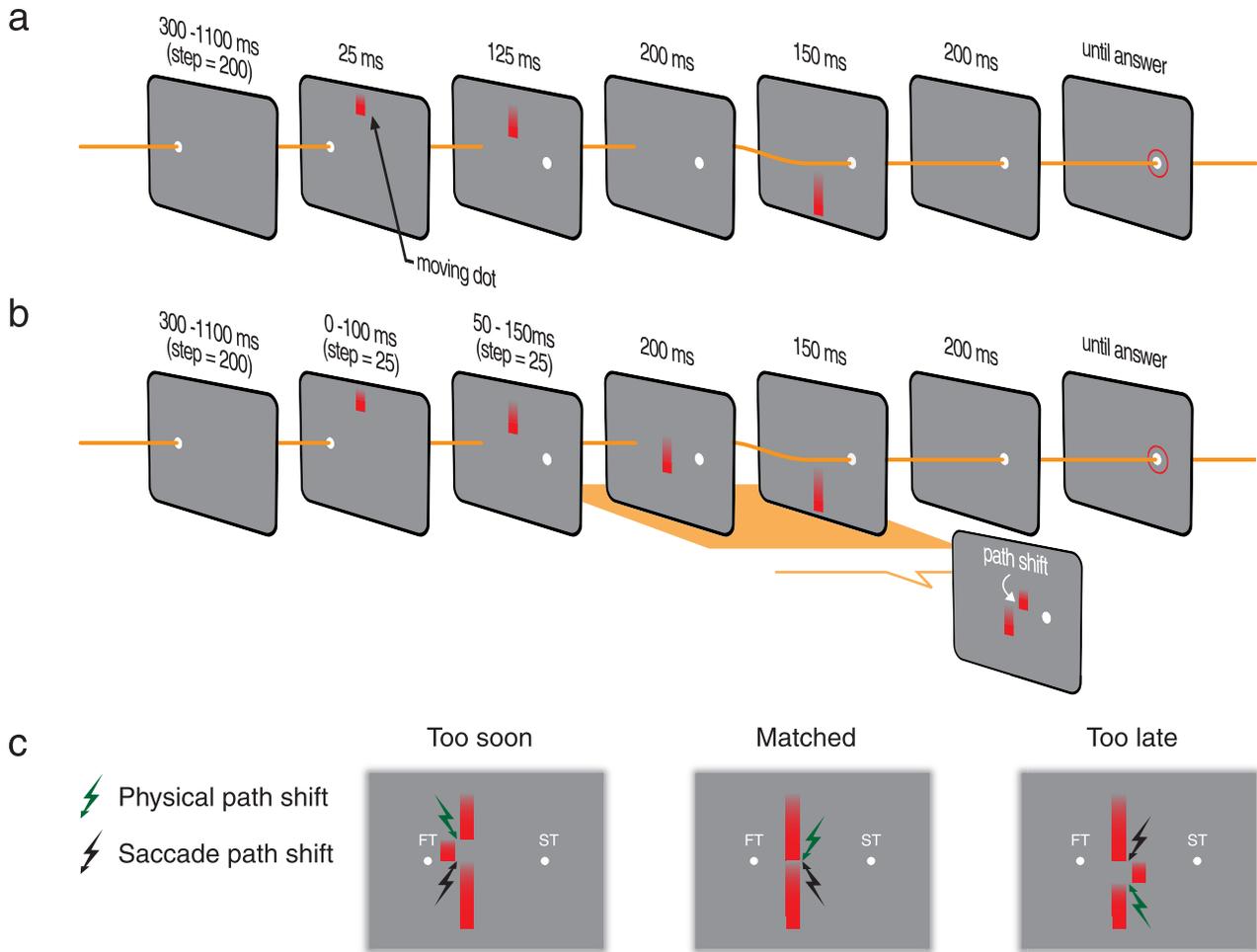
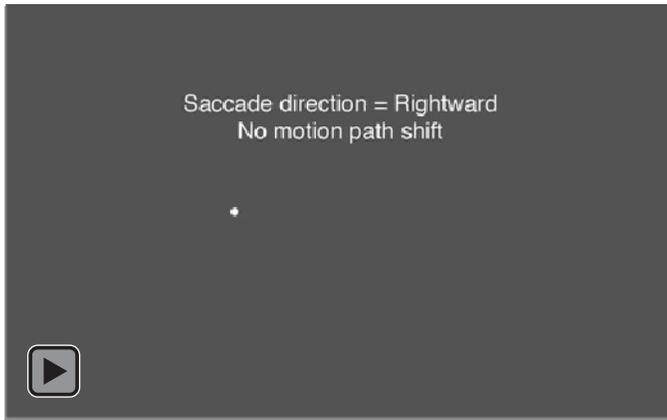


Figure 3. Stimulus sequences. The orange line represents the line of gaze during a rightward saccade trial. Shortly after the red dot began its downward motion, the white fixation spot jumped 15° to the right; observers were instructed to saccade rapidly to the new fixation location while simultaneously paying attention to the downward motion path. (a) In the first experiment, we measured the apparent offset between the pre- and post-saccadic vertical motion paths. A blank of 200 ms was inserted in the middle of the path to make any offset noticeable and easy to report. Observers reported whether they perceived the latter, lower motion trace (post-saccadic) to the left or right of the upper trace (pre-saccadic). (b) In the second experiment, we measured the time at which the offset occurred relative to the saccade. Observers again saccaded as soon as the white fixation dot shifted location. The downward motion of the red dot continued without blanking but its path was abruptly, physically shifted by the amount that should correct the pre- and post-saccadic misalignment, as measured in the first experiment. This physical path shift was introduced at different times relative to the saccade onset (orange area) and observers were asked to report whether the motion trace looked continuous or appeared to have breaks. (c) If the physical path shift preceded or followed the saccade-induced shift in time, observers saw two breaks (“Too soon” and “Too late”). The motion trace would be most likely to look continuous if the physical path shift matched the saccade-induced shift in both size and timing (see “Matched”).

We used multiple staircases to adjust the horizontal gap between the first and the second motion traces so that the physical offset nullled the saccade-induced misalignment. In order to do so, the horizontal position of the top and bottom motion paths were offset simultaneously in opposite directions. In each experimental block we ran four simultaneous staircases of 40 or 60 trials each (two staircases for rightward and two for leftward saccade trials), starting successively at one of six randomly chosen horizontal offsets between top and bottom motion paths that were

linearly spaced between $+2^\circ$ and -2° around the horizontal midpoint of the screen (negative values mean that the second motion trace was displayed to the left of the first one).

Trials were screened online based on the spatial properties of the saccade (started within 1.5° of the fixation target and ended within 2° of the saccade target) and the temporal properties (saccade should occur within the interval where the moving probe was blanked). Trials that didn't satisfy these criteria were randomly replaced later in the block and the trial



Movie 2. Stimuli from Experiment 1. This video contains three different examples of rightward saccade trials from the first experiment. First, fixate the white dot and press the play button on the bottom left corner of the movie. The red dot will start moving down the screen. Then, as soon as the white dot moves to the right, shift fixation to its new location. At the same time, notice whether the second, lower portion of the motion trace falls to the left or to the right of the initial, upper one. In the first sequence, both motion traces are aligned; in the second sequence, the second one is displaced in the opposite direction of the saccade (motion path shift: -13% of saccade size); in the third sequence the second motion trace is displaced in the direction of the saccade (motion path shift: $+13\%$ of saccade size).

outcome did not affect the current staircase. To familiarize observers with these criteria and with the task itself, they ran a block of 160 or 240 trials in which feedback on the saccade execution was given after each trial. No feedback was given during the experimental trials. The data obtained in the training blocks weren't taken into account for later analyses. Each observer ran the training block and three experimental blocks composed of 160 or 240 trials each (three observers ran 480 trials, the others ran 720 trials) in three different sessions. Each session was composed of one block and lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min.

Before proceeding to the behavioral analyses, we re-analyzed the fixation and saccade execution records following strict criteria (Results and Figure 4a). We then determined for each observer, and each saccade direction separately, the horizontal offset between motion traces that elicited the perception of two aligned traces. To do so we fitted cumulative Gaussian functions onto the proportion of “right” reports (i.e., the second, lower motion trace perceived to the right of the first, upper one) for each horizontal offset tested. We then determined the point of subjective alignment (PSA) corresponding to the level of 50% of “right” reports.

Results

In this first experiment, we evaluated the size of the horizontal offset between pre- and post-saccadic motion segments. To do so, we determined the horizontal offset between motion segments necessary for participants to perceive them as aligned across a saccade while masking the central portion of motion. Overall, 4,741 trials were run across all observers but of these, 901 were rejected online as falling outside the spatial and temporal criteria during the online analysis, leaving 3,840 selected trials. We then re-analyzed the eye-tracking data for these trials offline in order to keep those where observers' saccades were spatially accurate and fixation was maintained correctly throughout the 150 ms before and the 150 ms after the probe blank period (within a radius of 1.5° and 2° centered respectively on the fixation and the saccade target). This selection, added to the online detection of correctly timed saccades (during the probe blank), together with the rejection of blinks, allowed us to select trials during which the eye was steady for all of the 150 ms durations of both the pre- and post-saccadic motion traces. Across all observers, these offline analyses led us to reject a further 287 trials, leaving 92.5% of all trials selected online (3,553/3,840) and 74.9% of all trials (3,553/4,741). Figure 4a shows the outcome of the offline selection for the horizontal eye positions of 60 representative trials.

We plotted a psychometric function based on the reports from these correct trials to determine the perceived horizontal offset between the two motion traces. The offset at which “right” reports reached 50% defined the point of subjective alignment (PSA) where the pre- and post-saccadic traces appeared aligned. Psychometric curves for two representative observers and two directions of saccade are displayed in Figure 5a and the results observed for all observers are displayed in Figure 5b. Figure 5b shows that the perceived shift (opposite to the PSA that nulls it) of the pre-saccadic trace is in the direction opposite to the saccade. This is observed for each observer and direction of saccade as well as for the mean across all observers.

We found a main effect of the saccade direction on the PSAs ($F[1,5] = 14.69$, $p < 0.05$), confirming that the shift of the pre- versus post-saccadic trace is to the left for a rightward saccade and to the right for a leftward saccade. These observed biases imply that the corrections for the effect of the saccade on perceived location were too large (hypermetric or over-compensated). For example, the fitted curves for the first observer indicate PSAs of $-4.24^\circ \pm 1.18^\circ$ and $+3.0^\circ \pm 0.35^\circ$ for rightward and leftward trials, respectively, resulting an overcompensation of the saccade by about a quarter of the saccade amplitude. On all observers our results reflect a

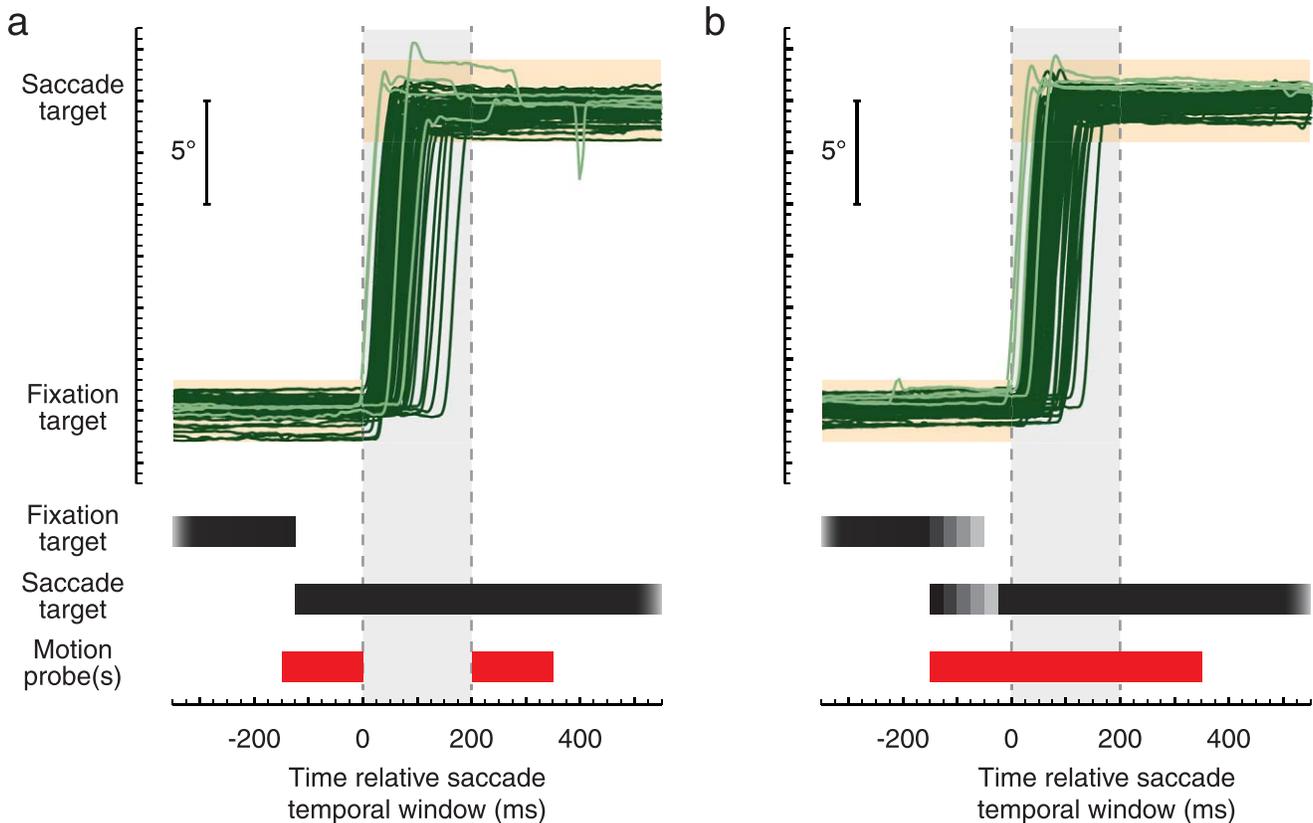


Figure 4. Trial selection. These graphs show 60 representative horizontal eye traces from all observers of the first (a) and the second experiment (b). In the first experiment, in order to select trials with saccades executed only within the 200 ms blank period, we used strict offline criteria (accurate fixation before and after saccade, correctly timed saccade, no blink, see text for more details) in addition to the online selection. We then kept the same criteria in the second experiment in order to compare similar saccade trial profiles. For both experiments, we sorted trials into two categories, “correct saccade” (dark green lines) and “incorrect saccade” trials (light green lines). Each “correct saccade” falls inside the saccade temporal window (gray area) and begins and ends within the acceptable pre- and post-saccadic spatial windows (light-orange areas). The bottom of each panel displays the presentations of the moving probe (red bars) as well as fixation and saccade targets (black bars). In [Experiment 2](#), the saccade target could appear at different times relative to the saccade temporal window; these different timings are represented in the right panel by the different levels of gray in the fixation and saccade target bars.

systematic overcompensation of 23.6% of the saccade amplitude (error of 3.54° for saccades of 15°).

Conclusion

This first experiment demonstrated that the observers perceived the motion trace of the probe in roughly spatiotopic rather than retinotopic coordinates with, nevertheless, a systematic error of compensation suggesting an over-correction of approximately one-fifth to one-quarter of the saccade amplitude. These properties of the compensation processes are similar to those observed previously with trans-saccadic apparent motion (Szinte & Cavanagh, 2011). For the initial motion trace to be seen in its actual spatial location, the persisting image of the pre-saccadic trace must be reassigned to a location shifted in the direction opposite

to that of the saccade by an amount equal to the saccade amplitude. Participants did not report seeing anything other than straight motion traces before and after the blanked out segment around the time of the saccade but that is to be expected given that the moving stimulus was not visible during the critical 200 ms before and after the saccade where compression is seen (Ross et al., 1997). The blanking allowed us to measure a baseline shift of the pre- vs. post-saccadic localization but also hid the path of remapping right around the time of the saccade.

Experiment 2

In our first experiment, we had evaluated the size of the horizontal offset between pre- and post-saccadic

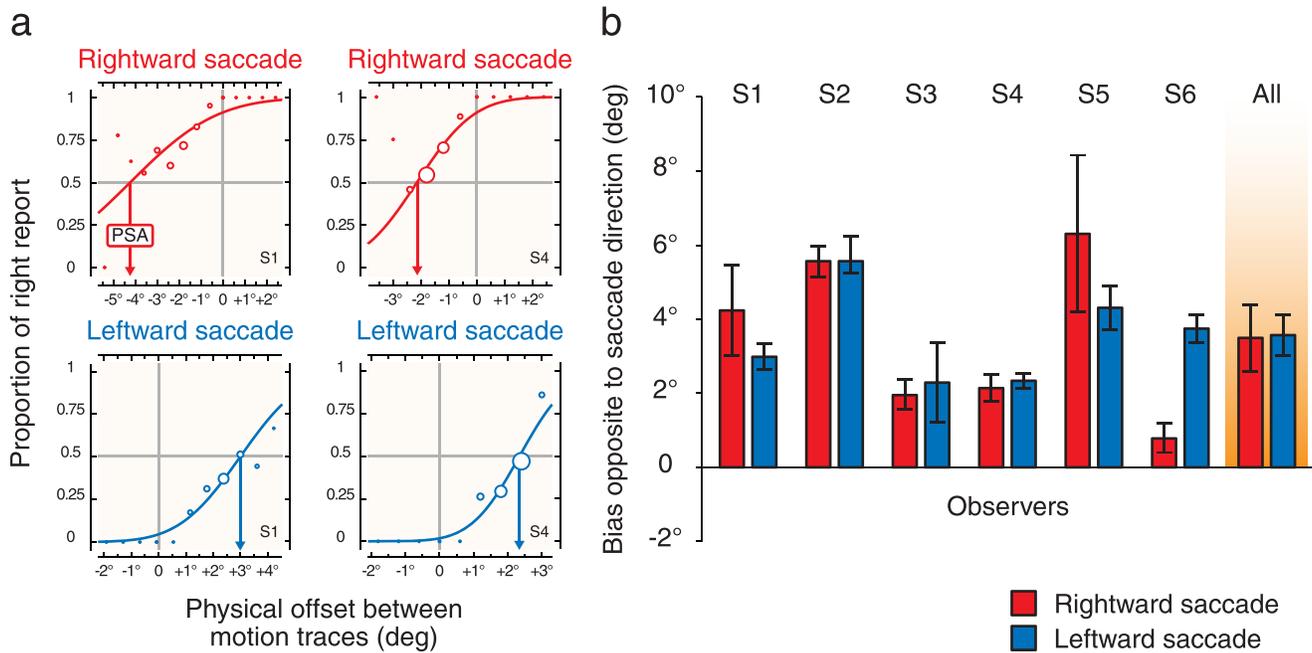


Figure 5. Individual and group results of [Experiment 1](#). (a) Proportion of “right” report in function of the physical offset presented between motion trace, for two representative observers for rightward (red curves) and leftward (blue curves) “correct saccade” trials. Psychometric functions were fitted to estimate the point of subjective alignment (PSA), i.e., the amount of horizontal physical offset between motion traces leading to equal response of “right” or “left” shift of the second motion trace relative to the first one. (b) Results for all observers and for the group. Bars represent the measured bias in the opposite direction of the saccade for each observers and saccade directions individually as well as the average across observers. Errors bars for each observer indicate 95% confidence interval computed by bootstrapping and the *SEM* for all observers.

segments of motion. This measure was used in this second experiment in order to cancel the offset and determine the timing of the perceived shift, if any.

Materials and methods

Observers, instruments, and stimuli

The observers, instruments and stimuli were the same as for the first experiment.

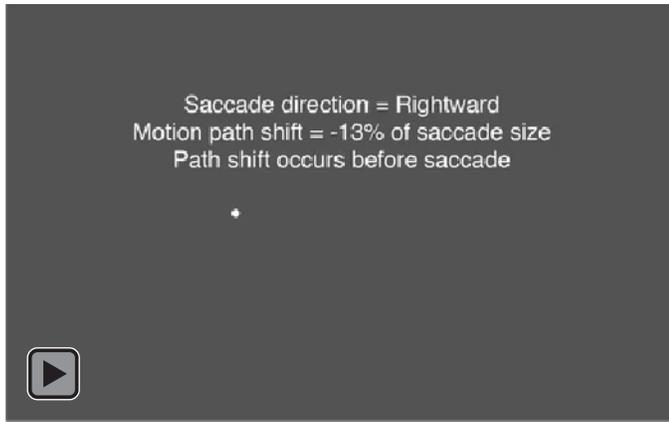
Procedure

The procedure for the second experiment was the same as for the first with the following exceptions. First, the moving dot continued in motion over its 25° path without being blanked. It was, however, offset at a particular moment during its descent. The shift that made the two segments appear aligned for each observer in [Experiment 1](#) was now introduced at various time points during its descent ([Figure 3b](#) and [Movie 3](#)).

To trigger saccades at different times relative to the probe shift, we presented the saccade target simultaneously with the disappearance of the fixation target at five random times between 0 and 100 ms (separated by

25 ms each) after the red dot began its downward motion. Using a method of constant stimuli we inserted the physical shift of the probe path equiprobable at one of 13 times between 100 ms and 400 ms after the probe appearance. Seven of these time points for the probe shift were distributed evenly between 100 ms and 400 ms (separated by step of 50 ms) after the probe appeared and began to move. To increase our sampling at the time of the saccade, we added six more time points at 8 ms intervals locked to the online detection of the saccade (average delay from detection to first probe shift was $14 \text{ ms} \pm 3 \text{ ms}$). Finally, 200 ms after the end of the motion sequence a red ring appeared around the saccade target indicating that observers should report whether the motion trace looked continuous, that is with or without break. We instructed observers to use the “continuous” response only if they saw an unbroken, straight motion trace.

We determined the correct execution of saccades online using the same criteria as in the first experiment and replayed randomly trials that did not satisfied these criterions. Each observer ran 20 experimental blocks of 26 correct trials each (520 correct trials), composed of equiprobable rightward and leftward saccade trials for the 13 possible times of the probe shift. Each observer ran four sessions composed of five blocks each that



Movie 3. Stimuli from Experiment 2. This video contains three different examples of rightward saccade trials from the second experiment. First, fixate the white dot and press the play button on the bottom left corner of the movie. The red dot will start moving down the screen. Then, as soon as the white dot moves to the right, shift fixation to its new location. At the same time, judge whether the motion trace looked continuous or not. In the first sequence the motion path shifts before the saccade target appears so two breaks should be seen: the physical shift followed by the saccade-induced shift; in the second sequence, the motion shift is presented around the time of a typical saccade and in this case the two shifts might cancel although this typically would require more exact matching of shift size and timing; finally, in the third sequence, the motion shift is presented long after the saccade target so that again, two shifts should be seen, in this case the saccade-induced shift followed by the physical shift. For these examples we used a motion shift of 13% of the saccade amplitude in the direction opposite to the saccade.

lasted less than 25 min each. During each session, the eye-tracking system was recalibrated every 8 min. Before proceeding to the behavioral analyses, we further screened the trials based on more stringent spatial and temporal criteria (Results and Figure 4b).

Results

We presented the moving dot before, during, and after the saccade so that any deviations occurring closer to the saccade could be seen. To determine if there was any deviation of the trajectory as might be predicted from the compression or peri-saccadic mislocalization results (Figure 2c-d), we asked observers to report if the trajectory appeared to be a continuous, linear trace. We already knew from Experiment 1 that the beginning and ending segments appeared misaligned, so we corrected the trajectory with a horizontal offset matched to each observer's measured offset. If there were major deviations corresponding to the compression or peri-saccadic mislocalization results, observers

would never report a continuous linear path. However, only breaks between linear segments were reported by participants. If the physical shift preceded or followed the saccade-induced shift in time, the participants saw two breaks, with the trace shifted first one way, and then back to the aligned beginning and end segments of the trace (Figure 3c, “too soon” or “too late”). The impression of continuous motion with no break required that the physical shift occurred at roughly the same time as (and in the opposite direction to) the saccade-induced shift (Figure 3c, “Matched”). In that case, all participants frequently reported seeing a continuous, linear trace. Depending on the observer, the maximum frequency at the peak of the Gaussian fit reached from 71% to 100% of trials at the optimal timing, with a mean maximum frequency of continuity reports at optimal timing of $85\% \pm 3\%$.

We determined for each participant and saccade direction the proportion of continuity reports of the motion trace for the different times of the physical shift latency relative to the saccade onset (in bins of 10 ms). We then evaluated the mean as well as the confidence interval of a normal Gaussian function fitted to the data. To take into account the different number of trials in each bin, we weighted the fit of the Gaussian by the number of trials that had been averaged into each datum point. The online analysis of the saccade led to rejection of 18.0% (683/3,803) of all trials as inaccurate, leaving 3,120 accepted trials. We then re-analyzed these accepted trials offline following the same stringent spatial and temporal criteria as in Experiment 1. We use the same temporal criteria, requiring saccade to be executed during the central 200 ms of the moving probe, corresponding to the blank period of Experiment 1, which now was not blank. Figure 4b displays the horizontal eye positions of 60 representative trials synchronized to the saccade temporal window onset. Across all observers these offline analyses led us to keep 92.7% of all trials selected online (2,891/3,120), corresponding to 76% of all trials (2,891/3,803).

Figure 6a displays, for two representative observers and for the two directions of saccade, the distributions of the continuity reports across different timings of the corrective shift relative to the saccade onset. For example, for the first observer with rightward saccades (upper left panel in Figure 6a), the maximum frequency of continuity reports occurs at 21.4 ± 5.7 ms after the saccade onset. This means that if the probe motion is presented 21 ms after the saccade onset with a horizontal shift of 4.24° in the opposite direction of the saccade (this observer's bias), then this observer reported seeing the probe move continuously down the screen more frequently than at any other timing, seeing no breaks or deviations in the motion trace. For each observer we determined the mean and the confidence interval of these Gaussian distributions and these values are shown in Figure 6b as well as the average

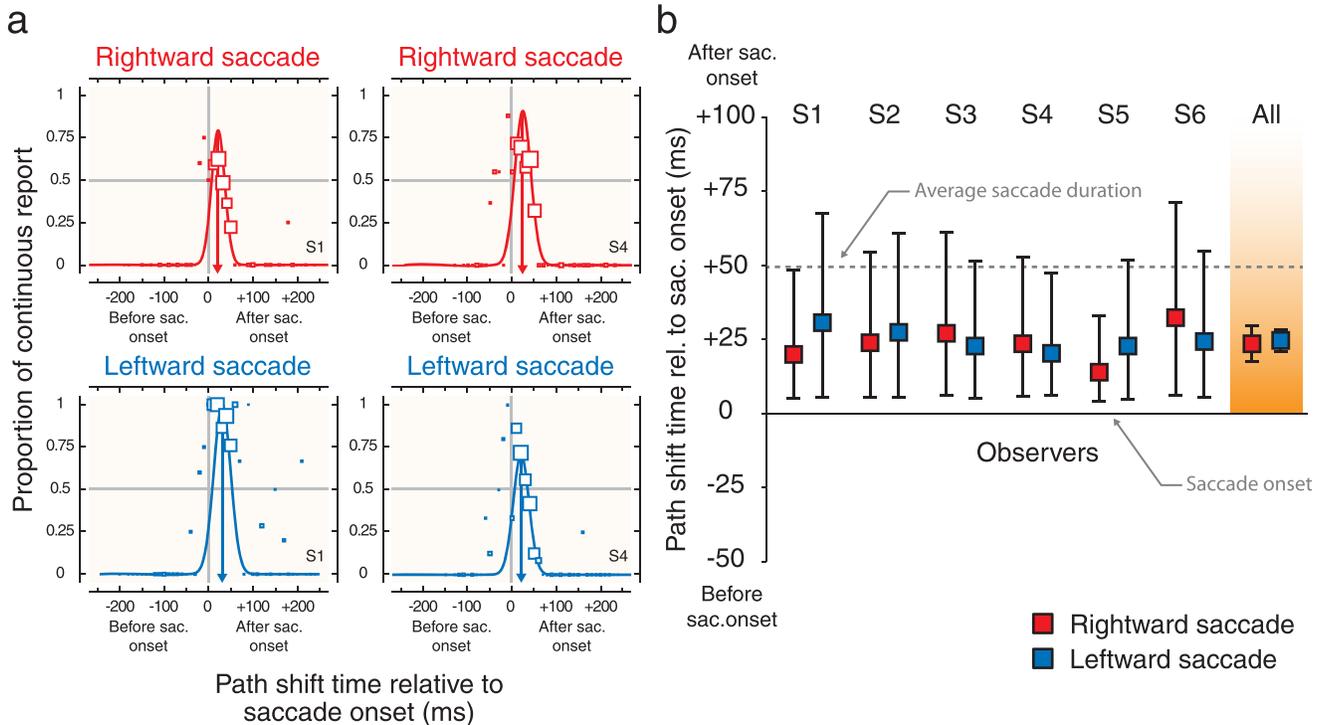


Figure 6. Individual and group results of Experiment 2. (a) Proportion of “continuous” motion reports as a function of the time of the motion path shift relative to the saccade onset, for two representative observers for rightward (red lines) and leftward (blue lines) “correct saccade” trials. The Gaussian functions fitting these data are weighted by the number of observations per bin. (b) Timing of maximum frequency of “continuous” reports (peaks of fitted Gaussians) for each observer and saccade direction and for the group. Error bars for individual observers indicate 95% confidence interval of the Gaussian distributions and the *SEM* for all observers.

across all observers. Results were highly similar across participants ($F[5,5] = 0.88$, $p = 0.55$) and no significant difference was observed between the two saccade directions tested ($F[1,5] = 0.13$, $p = 0.73$). Across observers and saccade directions, the peak frequency of continuity reports occurred at 24.4 ± 1.6 ms after the saccade onset. As illustrated in Figure 6b (see gray dashed line), the mean saccade duration was 48.9 ± 2.1 ms (median: 48.17 ± 2.1 ms), and no significant differences were observed for the mean or median saccade duration between participants (for the mean saccade duration: $F[5,5] = 2.92$, $p = 0.13$; for the median saccade duration: $F[5,5] = 2.49$, $p = 0.17$) or saccade directions (mean: $F[1,5] = 0.20$, $p = 0.67$; median: $F[1,5] = 0.09$, $p = 0.78$). The moment at which the pre-saccadic trace shifts therefore falls during the saccade flight, suggesting that at a perceptual level the compensation is in place when the saccade lands.

Conclusion

By presenting a physical offset in the motion path that nulled the error in saccade compensation, we were able to determine the moment at which the persisting pre-saccadic motion trace is shifted to its (almost)

appropriate spatiotopic location. Our results suggest that this process occurs at about 24 ms after saccade onset and that once this is corrected, no other deviations in the path were seen. That is, no deviations were reported that would correspond either to the large peri-saccadic mislocalization seen with single flashes (Honda, 1989; Matin & Pearce, 1965; Ross et al., 1997) or the small deviations previously reported by Honda (2006) in a similar moving probe design. However, these deviations of the visible motion may be masked by saccadic suppression (Burr, Holt, Johnstone, & Ross, 1982; Matin, 1974) and might be revealed at higher contrasts, a question we investigate in the next experiment. We also emphasize that the shift of the pre-saccadic portion of the trace is a repositioning of the entire persisting trace. It is this repositioned trace that has the linear feature that observers use to report the alignment or misalignment of the pre- and post-saccadic segments. Our data do not specify the duration of this repositioning, it may well start before the saccade and end after, we can only determine its midpoint, which is near the middle of the saccade. The position of the pre-saccadic motion trace can be reported both before and after the saccade, but there appears to be no experience of its displacement between these locations even though this entails a shift of several

degrees. As is the case for deviations of the moving dot itself around the time of the saccade, the visibility of this shift of the entire pre-saccadic motion trace may also be suppressed by the saccade.

Experiment 3

Results from Experiments 1 and 2 suggest that pre- and post-saccadic motion traces were seen as misaligned and that the pre-saccadic segment was mislocalized in the direction opposite to the saccade, relative to the post-saccadic segment, by approximately one-fifth of the saccade amplitude. In contrast, Honda's observers reported (by making drawings) that the pre- and post-saccadic trajectories were *aligned* and showed as well a small deviation at the time of the saccade (Figure 1). We therefore ran a final experiment to examine the effect of the remaining differences between our stimuli and Honda's: saccade target duration (in his case the saccade target stayed on during 20 ms, in ours, it stayed until the end of the trials, so for at least 600 ms); and the contrast of the moving probes (in his case 30 cd/m² on black background; in ours, 12 cd/m² on a background of 4.5 cd/m²). We changed our display to match these values as closely as possible and asked observers to report the relative horizontal difference (if any) of the pre- and post-saccadic motion traces. They did so, after the probe motion was finished, by moving two vertical lines to mimic the alignment they had seen. Also, at the end of the session, we asked them to draw the perceived trajectory as Honda did.

Materials and methods

Observers, instruments, and stimuli

Five volunteers from Université Paris Descartes took part in Experiment 3 (one author and four observers naïve to the purpose of the experiment, ages 22–37, four males and one female, two of who had participated in Experiments 1 and 2). All had normal or corrected-to-normal vision and gave informed consent. The experiments were carried out according to ethical standards specified in the Declaration of Helsinki.

The instruments and stimuli were the same as before except that the screen background was either black (0.1 cd/m²) or dark-gray (4.5 cd/m²). In the black screen background condition, we turned off the experimenter screen (eye-tracking control screen) in order to limit the external lights to the eye-tracker infrared lights and to the dim background of the CRT screen. Finally, saccades were detected online and re-analyzed offline using the same criteria as Experiments 1 and 2.

Procedure

The procedure for the first part of this experiment was the same as for Experiments 1 and 2 with the following exceptions. First, the probe contrast was increased on all trials by reducing the luminance of the screen background, from dark-gray to black. Second, although the duration of the fixation target, and probe were the same as in Experiment 1 (Figure 3a), the saccade target was either presented until the end of the trial (as in Experiments 1 and 2) or lasted only three monitor frames (25 ms, compared to 20 ms for Honda, 2006) leading respectively to “visible target” and “memory target” saccade trials which were equal in number and randomly intermixed. Next, the moving dot could either be continuously presented over its 25° path (as it was in Experiment 2 and Honda's experiments) or blanked in its central part (as it was in Experiment 1) leading to equal numbers of “blanked” and “continuous” motion trials in a random sequence. Moreover, contrary to Experiments 1 and 2, the motion probe always followed a continuous trajectory, directly down the display at the screen center without any shift in the path. At the end of each trial, we asked observers to report the horizontal offset between the top and bottom motion traces by adjusting with a computer mouse the horizontal location of two bars (7.5° by 1° each, 5° above and below the screen center, 1 cd/m²) presented sequentially at a random horizontal location between +3° and –3° around screen center. As before, saccades were screened online and trials that didn't satisfy our criteria were randomly replaced later. In order to be familiarized with our criteria and the task itself, observers ran a session of 80 trials in which feedback on the saccade execution was given. No feedback was given during the experimental trials. The data obtained in the training session weren't taken into account for later analyses. Each observer ran the training session and three experimental sessions composed of 80 trials each. Each session lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min.

Finally, after these adjustment trials, in the second part of the experiment, observers were presented a series of “drawing” trials with continuous motion of the probe where no adjustment responses were made. The observers were asked to focus on the whole motion trajectory and instructed to remember the perceived motion traces that they would later draw without having their head on the chin rest. We presented the trials in four blocks in random order. Each block had 15 identical trials composed of either rightward or leftward saccade trials and with contrast and saccade target similar either to our first and second experiments (“low contrast motion,” red probe on dark-gray background, visible target saccade) or to Honda's experiments (“high contrast motion,” red probe on

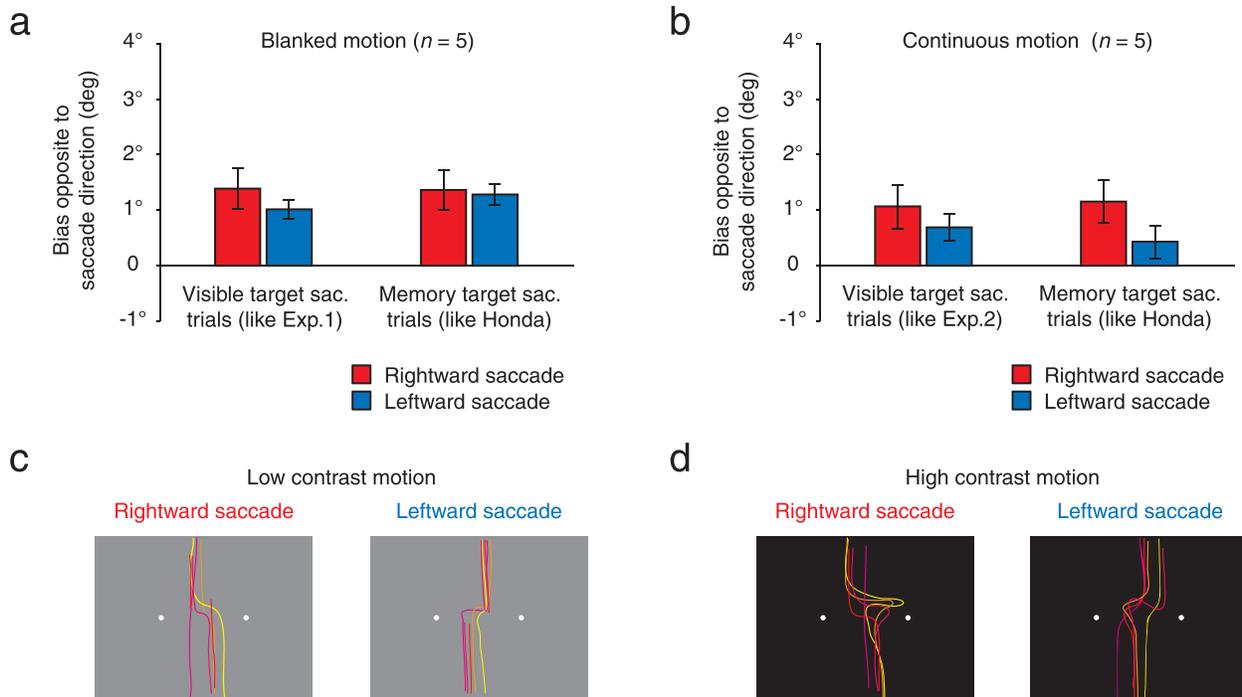


Figure 7. Group results of Experiment 3. (a) Bars represent the measured bias in the direction opposite that of the saccade, averaged across observers ($n = 5$) in the “visible target” saccade trials (like those of Experiment 1) and the “memory target” saccade trials (like those of Honda, 2006). Errors bars indicate the SEM. (b) Same observations for the continuous motion condition for the “gap saccade” trials (like those of Experiment 2) and the “memory saccade” trials (like those of Honda, 2006). Errors bars indicate the SEM. (c) This panel shows 10 representative drawings made by the observers in the low-contrast motion case in rightward and leftward saccade trials. The line colors from magenta to yellow are present to visually segment the reported traces. (d) Same observations for the high-contrast motion condition.

black background, memory target saccade). At the end of each block, observers drew five trials that they consider as the most representative of the 15 trials they had seen. Saccades were screened online and trials that did not satisfy our criteria were randomly replaced later. Feedback was given after each incorrect saccade trial and observers were instructed to ignore those trials in their later drawings. Drawings were collected on an electronic tablet using an electronic pencil and a drawing software (SketchBookPro for iPad, Autodesk, San Rafael, CA), saccade as well as fixation targets were presented on the drawing display and observers were familiarized with the device before running the experiment.

Results

We used the same online and offline saccade analysis as in Experiments 1 and 2. The online analysis rejected 25.7% (415/1,615) of the trials and the offline analyses rejected a further 11.4%, leaving 1,063 trials. Figures 7a and 7b show the average setting of offset between upper and lower bars for the “blanked” (moving probe not shown in middle 200 ms) and “continuous” (probe

always present) conditions, respectively. The size of the offset did not differ between “blanked” and “continuous” trials (two-tailed t -test, $t(4) = 2.571$, $p = 0.07$). In both cases, the pre-saccadic segment was seen shifted in the direction opposite to the saccade (relative to the post-saccadic segment). These results are consistent with the findings in Experiments 1 and 2, despite the differences in background contrast and measurement procedure.

More specifically in the blanked condition the pre-saccadic trace was on average perceived shifted $1.27^\circ \pm 0.09^\circ$ in the opposite direction to the saccade. Within those trials there were no significant differences between saccade directions ($F[1,12] = 1.011$, $p = 0.33$), or target durations (visible or memory saccade trials: $F[1,12] = 0.279$, $p = 0.61$) nor a significant interaction between these two factors ($F[1,12] = 0.446$, $p = 0.52$).

In the continuous condition, the pre-saccadic trace is on average perceived shifted $0.84^\circ \pm 0.17^\circ$ in the opposite direction to the saccade. Again there was no significant difference between saccade directions ($F(1,12) = 1.895$, $p = 0.19$), saccade target durations ($F(1,12) = 0.051$, $p = 0.82$) and no significant interaction between them ($F(1,12) = 0.183$, $p = 0.68$).

Making the stimulus parameters closer to Honda's did, however, affect the perceived trace right around the time of the saccade (in the continuous condition). Here, the drawings of observers showed that some observers (two of five) saw in some trials a deviation in the trace, when the probe had high contrast but never at low contrast. However, even when the excursion was reported, observers do not see an alignment between the top and bottom motion trace as can be observed in [Figure 7d](#). Even in these drawings with a visible peri-saccadic excursion in the trace, observers still report an offset between pre- and post-saccadic segments that is similar in direction and amplitude to that measured just before with the alignment test.

Finally, it is interesting to note that with the higher contrast (and a different method of measurement), the measured biases were smaller than those from [Experiment 1](#). This suggests that drawing attention to the path of the peri-saccadic motion trace might distract attention from the misalignment judgment, making it the less noticeable (a kind of change blindness).

Conclusion

These results demonstrated again that when a saccade occurs while an object is moving, the motion path does not conform to the path the object takes across the retina. Instead, it is perceived in roughly spatial coordinates, with, however, a systematic overcompensation of the saccade amplitude. This misalignment is seen in all of our experiments. In [Experiment 3](#) with higher contrast, some observers also reported a deviation in the path around the time of the saccade, recovering one aspect of the findings in Honda's (2006) paper that was not reported by our observers with the lower contrast probe used in [Experiment 2](#). Since the speed on the retina during the saccade is quite fast, it is reasonable that the deviations of the low-contrast probe in [Experiment 2](#) might be missed, especially as it would occur during the interval of maximum saccadic suppression (Burr et al., 1982; Matin, 1974). Despite the visibility of the peri-saccadic excursion at high contrast, our observers, unlike Honda's, still reported the misalignment of the pre- and post-saccadic segments.

General discussion

We used a probe that moved on a linear path before, during, and after a saccade to visualize the dynamics of saccade compensation. The pre-saccadic portion of the trace was not seen to jump in the direction of the saccade as it does on the retina ([Figure 2b](#)); nor did it

make a curve toward the saccade target and then back to the spatial path ([Figure 2c](#)) as would be expected from peri-saccadic compression (Ross et al., 1997) or a three-part curve ([Figure 2d](#)) as expected from peri-saccadic mislocalization (Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). Instead, the continuous motion trace was seen as two misaligned but linear segments, with the pre-saccadic segment shifted in the direction opposite to the saccade ([Figure 2e](#)). This first observation also differed from an earlier report by Honda (2006) using a similar moving probe technique. His observers, using drawing as a measure, reported that the pre- and post-saccadic segments appeared generally aligned and had, in some cases, a small, brief excursion at the time of the saccade. When we increased the contrast of our moving probe, some of our observers did report small excursions around the time of the saccade but even so, all our observers continued to see the pre- versus post-saccadic misalignment. We conclude that the moving probe does not provide any better access to fine-scale peri-saccadic mislocalization than a static flickering probe—that is to say, almost none at all. Apparently, the continuous, pre-existing position reference provided by the moving probe overrides any mislocalization that would be suffered by individual flashes or by flash sequences or motion traces beginning before the saccade (Sogo & Osaka, 2001; Watanabe et al., 2005). Nevertheless, the moving trace does reveal a large-scale mislocalization only previously reported in an apparent motion procedure (Szinte & Cavanagh, 2011) and it does so consistently across three different experimental procedures.

To characterize the timing and magnitude of this trans-saccadic misalignment, we first determined the horizontal offset between the pre- and post-saccadic segment of the moving probe while the central segment was blanked. In our procedure measurements were always made by relative judgments of the post- against the pre-saccadic trace. When the motion trace was actually aligned along its entire length, observers saw the pre-saccadic segment as shifted relative to the post-saccadic segment (shifted in the direction opposite that of the saccade). To bring the two segments into alignment, observers had to physically shift the post-saccadic segment, also in the direction opposite that of the saccade, by approximately one-fifth of the saccade amplitude (about 18° compensation for a 15° saccade). This result indicated that the pre-saccadic motion trace was corrected for the effect of the saccade and perceived in roughly spatiotopic rather than retinotopic coordinates. An accurate correction would have shifted the pre-saccadic trace by the entire length of the saccade; however, the effect of the saccade was overcompensated (hypermetric), moving the pre-saccadic trace too far.

We then introduced a horizontal shift in the continuous trace to cancel the over-correction and asked observers to report if the motion trajectory appeared to be a continuous linear trace or not. If the moving probe were physically offset at roughly the same time as the saccade-induced shift, observers would have an impression of continuity (if no other deviations from linearity were caused by the saccade). By evaluating the time profile of the continuity reports we identified the moment at which the pre-saccadic trace was shifted to its appropriate, nearly spatiotopic location. We found that this process occurs at about the midpoint of the saccade, suggesting that at a perceptual level the compensation is in place when the saccade lands.

We finally compared our results to a study reporting no misalignment between the pre- and post-saccadic trace (Honda, 2006). However, even with settings similar to those used in Honda's study, we still found the same misalignment. This misalignment remained even at high probe contrast when the peri-saccadic excursion that Honda had reported became visible.

How could we explain the perceived motion shift?

Perceptually, the pre-saccadic half of the motion trace is seen shifted, relative to the post-saccadic half, in the direction opposite to that of the saccade (Movie 1). However, this is a relative judgment that cannot assess whether the first, second or both segments shifted. It would seem that logically the shift should be attributed to the pre-saccadic trace, which needs to be corrected in order to appear relatively near its true spatial location; the second, continuing segment motion should be seen at the location corresponding to its retinal position as is the rest of the experimental scene. We have used the term “remapping” (Duhamel et al., 1992) to describe this correction of the pre-saccadic segment. Physiologic remapping is described as an anticipatory response in cells that will receive the target input after the saccade and the perceived correction of location in our experiments here may well be mediated by physiologic remapping. However, our experiment does not test any link between the physiologic remapping and our behavioral measures. Nevertheless, our results of an overcompensation may provide such a link if similar deviations in the location of remapping activity are found in single cell recordings. In addition to the amount and direction of the spatial correction, our results also offer a temporal profile of the correction and localize it to the midpoint of the saccade itself. The distribution of timings we see do extend before and after the saccade, as does the remapping activity (Duhamel et al., 1992; Goldberg & Bruce, 1990;

Kusunoki & Goldberg, 2003; Umeno & Goldberg, 1997) although given the many factors that contribute to the shape of our “continuity” reports we do not place much weight on this.

This “remapping” correction is based on efference copy (von Holst & Mittelstaedt, 1950), an oculomotor command signal that, depending on the theory, acts on the whole visual field to detect and correct any change (von Helmholtz, 1867), or acts on a limited number of attended targets (Cavanagh et al., 2010; Wurtz, 2008), or is used to generate a spatiotopic map (Bischof and Kramer, 1968; Breitmeyer et al., 1982). An alternative mechanism to achieve visual constancy, the “reference object” theory (Bridgeman, 2007; Bridgeman, Van der Heijden, & Velichkovsky, 1994), operates post-saccadically, comparing a memory of the saccade target to the post-saccadic configuration to locate the original saccade goal and shift spatial coordinates to align with it. However, our results here suggested that the compensation of coordinates is already in place by the end of the saccade, giving little time for a “reference object” process to operate. Nevertheless, given that perception occurs with a substantial delay, this backdating of the correction is not a significant challenge to the reference object theory.

Whatever the mechanism producing the correction, we found a consistent error that was visible as a misalignment of the pre- and post-saccadic segments of the motion trace. Interestingly, this consistent error does not seem to be attenuated over time even though a mismatch between the expected and actual post-saccadic locations typically leads to rapid adaptation that minimizes this offset (Collins, Rolfs, Deubel, & Cavanagh, 2009). This saccadic adaptation effect is classically found for the saccade target itself whereas our target of interest was midway between the saccade goal and fixation. We should also point out, the adaptation is seen by many, though not all (Awater, Burr, Lappe, Morrone, & Goldberg, 2005), as a change in the motor response, not perception. Although these may be reasons for the absence of adaptation of the perceived locations in our experiments, another is that this persistent trans-saccadic shift has different values at different locations in the visual field (Szinte & Cavanagh, 2011), being an overcompensation at some locations and an undercompensation at others. These location-specific biases were quite stable over time in that earlier experiment and that raises the issue that not all of these shifts can be corrected by a common factor, and the remaining shifts may be the residual after the common factor is removed. However, since we tested the visible shift only at one location in this experiment, we cannot make any generalizations.

The timing of the shift, measured in our second experiment, appears to fall directly in the middle of the saccade itself, although this result specified only the time of the midpoint of the correction process, not its

duration. In that second experiment, we added a physical shift to offset the saccade-induced shift, and we based the size of this correction on the shift measured when there was a large gap in the central portion of the path (from [Experiment 1](#)). It is certainly possible that the size of the saccade-induced shift might be affected by the presence of that gap. In particular, Deubel and colleagues (1996) showed that adding a blank after the saccade improves the detection of a displacement of the saccade target. Nevertheless, the frequency of continuity reports reached extremely high values at the optimal timing (85% on average) suggesting that the amplitude of the correction that we used was appropriate and that the gap in the motion path did not affect the amount of perceived shift.

We might be concerned in the conditions with continuous motion traces ([Experiment 2](#)) that saccadic suppression (Bridgeman, Hendry, & Stark, 1975; Burr, Holt, Johnstone, & Ross, 1982; Matin, 1974) might mask the visibility of any displacements such as the physical path shift that we introduced into the trajectory near the time of the saccade and so account for the reports of continuity. In particular, when the physical step occurred very near the time of the saccade, its combination with the saccade-induced shift might produce a complex path that would not be seen because of saccadic suppression. It may well be smoothed out or filled in (see drawings). Despite the possible loss of details right around the time of the saccade, it is nevertheless clear that to cancel the otherwise visible saccade-induced shift, the physical counter-shift should be placed at or near the moment of the saccade itself. The physical shift and the uncorrected saccade shift became visible as soon as the physical shift occurred 50 ms before or after the saccade, indicating that the saccade-induced shift must be occurring within that window. Although saccadic suppression may obscure the details of the motion trace and its correction right around the time of the saccade, it does not suppress the misalignment seen between pre- and post-saccadic segments. These segments extend well beyond the range of saccadic suppression and when the pre- and the post-saccadic motion traces were actually aligned, saccadic suppression did not prevent our observers from seeing a displacement in the path.

Monitor persistence, retinal motion, and foveal bias factors

Could the observers' reports of a motion trace almost aligned in spatial coordinates (rather than retinal) have been a result of monitor persistence (Jonides, Irwin, & Yantis, 1982, 1983)? Clearly not, as any persisting trace on the monitor would have to be aligned over its whole length, independently of the

saccade, a result that our observers never reported. Nor did retinal persistence appear to play any role as the retinal trace of the pre-saccadic motion path would be moved to the other side of the saccade target where it was never observed.

Could the retinal motion of the visual probe during the saccade contribute to the shift of the pre-saccadic trace and or its misalignment? Retinal motion of the probe could not be a factor in [Experiment 1](#) where the probe was not present during saccade. Moreover, there was no effect of presence or absence of the probe during the saccade in [Experiment 3](#) (blanked vs. continuous conditions). Overall, we have no evidence of that the probe's motion over the retina during the saccade contributes to the under-correction or over-correction of pre-saccadic locations.

Finally, we cannot entirely exclude the role of foveal bias (Mateeff & Gourevich, 1983; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999) where brief duration stimuli are seen closer to the fovea than long duration stimuli. If our pre-saccadic and post-saccadic probes are both seen closer to the fovea's location at the time of their presentation, this could, given a few other assumptions, mimic the direction of our effects. However, foveal bias has been reported only for briefly flashed, static stimuli whereas our moving probes were present for 150 ms ([Experiments 1 & 3](#), blanked condition) or about 250 ms ([Experiment 2](#) and the continuous condition of [Experiment 3](#)) before and after the saccade. In a previous study where we assessed the contribution of foveal bias directly for a trans-saccadic apparent motion stimulus, we found that it could explain no more than 20% of the pre- vs. post-saccadic misalignment (Szinte & Cavanagh, 2011).

What about mislocalization and compression?

In contrast to our pre- vs. post-saccadic misalignment (10% to 20% of saccade amplitude) and small peri-saccadic excursions (seen by some observers in [Experiment 3](#)), peri-saccadic mislocalization and compression effects (Lappe et al., 2000; Matin & Pearce, 1965; Ross et al., 1997) can be as large as the saccade itself. In these studies, a single, brief probe was presented around the time of the saccade and participants reported the perceived location of the probe after making the saccade. When the probe is located between fixation and the saccade target, it will appear increasingly shifted toward the saccade target in the 100 ms preceding the saccade, to be then shifted back in the opposite direction, returning to its veridical spatial location by about 100 ms after the saccade for the compression literature ([Figure 2c](#)), while for peri-saccadic mislocalization ([Figure 2d](#)), the path after the

saccade should deviate back toward the fixation target before returning to the actual path (Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). If any of these processes acted on our moving probe, it should have been seen to deviate toward the saccade target just prior to the saccade to then return to the veridical path just after it (Figure 2c) or after an opposite deviation toward the fixation (Figure 2d). The duration of this excursion would take up 20% to 40% of our motion path and so it would be difficult to miss in our continuous trace condition.

The critical difference between the two tasks is that, in our case, the probe is continuously present whereas in mislocalization and compression tasks, there is only a single, brief probe. It is possible that our continuous stimulus provides a reference for each new, slightly shifted point in the motion path, providing a landmark to stabilize the perceived location across the saccade. For example, Schlag and Schlag-Rey (1995) reported that a single point of light was seen as a streak if presented only during the saccade, but was stable and well localized if its presentation extended before or after the saccade. Honda (2006) also reported that largest mislocalization occurred when motion occurred right around the time of the saccade and found that little or no peri-saccadic mislocalization and compression when the duration of probe's motion extended before or after the saccade by 100 ms or more. Thus the stable location information of a continuously present, flickering probe appears to override the labile position information of the brief flashes and this effect of “grandfathering in” for well-defined position appears to hold for a moving probe as well, where the position, although changing, is predictable from one moment to the next.

However, this “grandfathering” effect did not override the large-scale misalignment (large-scale in terms of time, pre- vs. post-saccadic). Nor did any “filling-in” or saccadic suppression of displacement act to obscure the misalignment. Since our motion followed a linear path, we might imagine that continuity processes would “fill in” any gap of reduced visibility created by saccade, similar to the filling in seen for lines that stretch across the blind spot. However, our motion probe, when not corrected for the saccade-induced shift, was neither stable nor filled-in across the saccade. It had a significant, pre- to post-saccadic misalignment of about 10% to 20% of the saccade amplitude. The transition between the two segments was sometimes seen as a discrete break, and sometimes as a sharp curve, but the two segments were invariably seen as misaligned. In contrast, pre-existing spatial references appear to remove or attenuate the large but transient variations of the perceived location of brief probes (Jeffries, Kusunoki, Bisley, Cohen, & Goldberg, 2007; Van Wetter & Van Opstal, 2008).

Conclusion

Using a continuous motion probe, we captured and made directly visible a gross and continuing misalignment of perceived location that occurs around the time of the saccade. The perceived location of the trace was shifted at about the midpoint of the saccade. The shift carried the persisting trace of the pre-saccadic motion about 20% too far suggesting an over-compensation for the effects of the saccade.

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References

- Awatramani, H., Burr, D., Lappe, M., Morrone, M. C., & Goldberg, M. E. (2005). Effect of saccadic adaptation on localization of visual targets. *Journal of Neurophysiology*, 93(6), 3605–3614.
- Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychological Research*, 32(3), 185–218.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Breitmeyer, B. G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. *Acta Psychologica*, 52(3), 175–196.
- Bridgeman, B. (2007). Efference copy and its limitations. *Computers in Biology and Medicine*, 37(7), 924–929.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during

- saccadic eye movements. *Vision Research*, 15(6), 719–722.
- Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences*, 17(2), 247–258.
- Burr, D. C., Holt, J., Johnstone, J. R., & Ross, J. (1982). Selective depression of motion sensitivity during saccades. *Journal of Physiology*, 333, 1–15.
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, 14(4), 147–153.
- Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision*, 9(5):29, 1–9, <http://www.journalofvision.org/content/9/5/29>, doi:10.1167/9.5.29. [PubMed] [Article]
- Cornelissen, F. W., Peter, E. M., & Palmer, J. (2002). The Eyelink toolbox: Eye tracking with MATLAB and the psychophysics toolbox. *Behavior Research Methods, Instruments, & Computers*, 34(4), 613–617.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, 36(7), 985–996.
- Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255(5040), 90–92.
- Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences*, 103(18), 7192–7197.
- Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, 64(2), 489–508.
- Hershberger, W. (1987). Saccadic eye movements and the perception of visual direction. *Attention, Perception, & Psychophysics*, 41(1), 35–44.
- Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics*, 45(2), 162–174.
- Honda, H. (2006). Achievement of transsaccadic visual stability using presaccadic and postsaccadic visual information. *Vision Research*, 46(20), 3483–3493.
- Jeffries, S. M., Kusunoki, M., Bisley, J. W., Cohen, I. S., & Goldberg, M. E. (2007). Rhesus monkeys mislocalize saccade targets flashed for 100ms around the time of a saccade. *Vision Research*, 47(14), 1924–1934.
- Jonides, J., Irwin, D. E., & Yantis, S. (1982, January 8). Integrating visual information from successive fixations. *Science*, 215(4529), 192–194.
- Jonides, J., Irwin, D. E., & Yantis, S. (1983). Failure to integrate information from successive fixations. *Science*, 222(4620), 188.
- Kusunoki, M., & Goldberg, M. E. (2003). The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *Journal of Neurophysiology*, 89(3), 1519–1527.
- Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, 403(6772), 892–895.
- Mateeff, S., & Gourevich, A. (1983). Peripheral vision and perceived visual direction. *Biological Cybernetics*, 49(2), 111–118.
- Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, 81(12), 899–917.
- Matin, L., & Pearce, D. G. (1965, June 11). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science*, 148(3676), 1485–1488.
- Müsseler, J., van der Heijden, A. H. C., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perception & Psychophysics*, 61(8), 1646–1661.
- Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Ross, J., Morrone, M. C., & Burr, D. C. (1997, April 10). Compression of visual space before saccade. *Nature*, 386, 598–601.
- Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research*, 35(16), 2347–2357.
- Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly; Delays and localization errors in the visual system. *Nature Reviews Neuroscience*, 3(3), 191.
- Sogo, H., & Osaka, N. (2001). Perception of relation of stimuli locations successively flashed before saccade. *Vision Research*, 41(7), 935–942.
- Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision*, 11(2):4, 1–20, <http://www.journalofvision.org/content/11/2/4>, doi:10.1167/11.2.4. [PubMed] [Article]
- Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I.

- Predictive visual responses. *Journal of Neurophysiology*, 78(3), 1373–1383.
- Van Wetter, S. M. C. I., & Van Opstal, A. J. (2008). Experimental test of visuomotor updating models that explain perisaccadic mislocalization. *Journal of Vision*, 8(14):8, 1–22, <http://www.journalofvision.org/content/8/14/8>, doi:10.1167/8.14.8. [PubMed] [Article]
- von Helmholtz, H. (1867). *Handbuch der physiologischen Optik*. Leipzig: Leopold Voss.
- von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften*, 37, 464–476.
- Watanabe, J., Noritake, A., Maeda, T., Tachi, S., & Nishida, S. (2005). Perisaccadic perception of continuous flickers. *Vision Research*, 45(4), 413–430.
- Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63(8), 1293–1313.
- Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics*, 63(8), 1314–1329.
- Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, 48(20), 2070–2089.