

Transsaccadic perceptual fusion

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Transsaccadic perceptual fusion is the integration of pre- and postsaccadic images into a single *percept* aligned in spatial coordinates. Several early studies reported an absence of transsaccadic fusion between dissimilar patterns, effectively stopping research on this question for three decades. We have now corrected two problematic aspects of these earlier studies and find robust evidence for transsaccadic perceptual fusion. First, we used simple pre- and postsaccadic targets, (|, ≡) for which spatial alignment is not critical. Second, we reduced the contrast of the postsaccadic stimulus, so that it would not suppress fusion. Participants reported seeing a superposition of the pre- and postsaccadic targets on 67% of trials. Importantly, we obtained similar results when the two stimuli were presented without an intervening eye movement, suggesting the existence of a general fusion mechanism. Directional biases in the saccade condition suggest that remapping might be the mechanism realigning the pre- and postsaccadic locations. Remapping may thus not only predict where targets will be located after a saccade but may also guide content, predicting what targets will look like. However, the constraints on the appearance of the fused percept suggest that it plays, at best, a limited role in visual stability across saccades.

retinal image and needs to identify and locate the items of interest. This processing might begin from a blank slate, as if seeing each image for the first time; alternatively, the carryover of information across the eye movement could provide computational benefits. However, numerous studies showed that the carryover of information is sparse. We are blind to most changes of an image across eye movements or other interruptions except for changes to previously attended items (Jensen, Yao, Street, & Simons, 2011; O'Regan, Rensink, & Clark, 1999; Simons & Ambinder, 2005). Based on this change blindness work, it would seem that most of the scene is processed anew after each eye movement. This would require some kind of mechanism to establish a correspondence between pre- and postsaccadic locations of the same object and allow visual stability. Early proposals as to how this stability was achieved assumed that the postsaccadic image was fused with a lingering presaccadic image. This fusion across multiple fixations formed a single, highly detailed, spatiotopic percept of the visual scene (e.g., Banks, 1983; Breitmeyer, Hoar, Randall, & Conte, 1984; Breitmeyer, Kropfl, & Julesz, 1982; Feldman, 1985; Jonides, Irwin, & Yantis, 1982; Trehub, 1977). For example, Wolf, Hauske, and Lupp (1980) reported that a sinusoidal grating presented before a saccade could still be seen briefly after the saccade at the same spatial location even if it had been removed before the saccade landed. Jonides et al. (1982) reported that partial matrices of dots were combined across eye movements. However, subsequent studies showed that both of these results were due to the phosphor

Introduction

We move our eyes about three times every second. With each eye movement the visual system receives a new

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persistence on the cathode ray tube (CRT) monitors rather to transsaccadic fusion (Irwin, Zacks, & Brown, 1990; Jonides, Irwin, & Yantis, 1983). In addition to these methodological issues, the perceptual fusion hypothesis then faced a series of studies that demonstrated a complete absence of transsaccadic fusion at the perceptual level. In particular, observers were unable to identify patterns when two halves are presented successively before and after a saccade (Bridgeman & Mayer, 1983; Irwin, Yantis, & Jonides, 1983; O'Regan & Levy-Schoen, 1983; Rayner & Pollatsek, 1983). This has commonly been taken as evidence that visual carryover across saccades does not occur.

In contrast, several studies report that pre- and postsaccadic representations interact with their postsaccadic representations in a number of ways: to create motion (Fracasso, Caramazza, & Melcher, 2010; Szinte & Cavanagh, 2011) or improve detection (Melcher & Morrone, 2003), to prime recall (Demeyer, De Graef, Wagemans, & Verfaillie, 2009; Pollatsek, Rayner, & Collins, 1984), support change detection (Hollingworth & Henderson, 2002), and bias perceived color (Oostwoud Wijdenes, Marshall, & Bays, 2015; Wittenberg, Bremmer, & Wachtler, 2008) among other effects. Transsaccadic tilt aftereffects have also been reported (Cha & Chong, 2014; Melcher, 2005; 2007; Zimmermann, Morrone, Fink, & Burr, 2013) although not replicated (Knäpen, Rolfs, & Cavanagh, 2009; Mathôt & Theeuwes, 2013). Given the early studies claiming an absence of transsaccadic perceptual fusion (Bridgeman & Mayer, 1983; Irwin, 1993; Irwin et al., 1983; O'Regan & Levy-Schoen, 1983; Rayner & Pollatsek, 1983), these findings were often interpreted mainly as memory-based effects where the presaccadic stimulus would interact with the activity of the postsaccadic stimulus (Demeyer et al., 2009; Irwin et al., 1990) without being perceived after the saccade.

Closer to our own experiments here, two recent studies have demonstrated a nearly optimal updating of presaccadic representation when a similar postsaccadic stimulus of reduced contrast is presented (Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015). It is quite possible that this improvement is based on a persisting perception of the presaccadic stimulus that is integrated with the postsaccadic one. However, because the pre- and postsaccadic stimuli are so similar (except for contrast), we cannot distinguish between memory-based improvement and perceptual summation as the result in either case is simply a stronger visible pattern. In the experiments here, we use two highly dissimilar patterns so that any perceptual persistence from the presaccadic stimulus can be seen and reported and either integrated with the postsaccadic pattern (perceptual fusion) or simply replaced by it (no fusion).

In the current study we sought to revisit transsaccadic perceptual fusion. We believe that the earlier

studies showing an absence of fusion were doomed to fail for methodological reasons. By modifying two crucial aspects of the methodology, we demonstrate transsaccadic perceptual fusion with highly dissimilar pre- and postsaccadic stimuli.

First, the stimuli used in earlier investigations required precise spatial alignment between the pre- and postsaccadic segments. In three studies (Bridgeman & Mayer, 1983; Irwin et al., 1983; Rayner & Pollatsek, 1983), participants were required to mentally fuse two halves of a dot matrix. Participants in O'Regan and Levy-Schoen's study (1983) had to integrate two sets of random line segments that formed three-letter words when superimposed. Any misalignment between the pre- and postsaccadic segments would make the dots or words impossible to identify even if there were transsaccadic perceptual fusion. Second, the high-contrast postsaccadic stimulus might have overpowered the weaker, pre-saccadic percept, defeating fusion. This might be related to the transsaccadic, spatiotopic masking that has been reported in several studies (De Pisapia, Kaunitz, & Melcher, 2010; Germeys, De Graef, Van Eccelpoel, & Verfaillie, 2010; Irwin, 1992a; McRae, Butler, & Poppel, 1987).

In contrast to these previous studies, we used simple probes where spatial alignment was not critical: a vertical bar before the saccade followed by a set of three horizontal bars after the saccade. Participants reported whether they saw none, one, or both stimuli at saccade offset and, if both, whether they appeared in succession or appeared fused as if superimposed. If the two halves appeared fused, we asked participants to report whether the vertical bar appeared to the left or right of the center of the three horizontal bars (Figure 1, inset). We also reduced the contrast of the postsaccadic stimulus to minimize the possibility that it might mask the presaccadic percept.

We also investigated to what extent the physical offset between the pre- and postsaccadic targets influenced the fused percept by varying the location of the (presaccadic) vertical bar relative to the center of the (postsaccadic) horizontal bars. Finally, to determine the potential influence of saccade metrics on the fusion between pre- and postsaccadic targets, we analyzed perceptual responses as a function of saccade landing position.

Methods

Participants

Six participants (all females; aged 20 to 34 years) performed the experiment. They were either students of the University of Paris Descartes or recruited via an

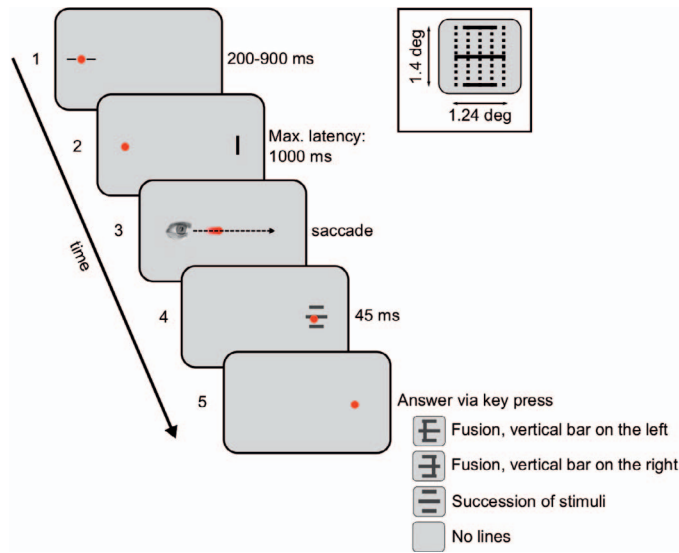


Figure 1. Protocol for one saccade trial. Each trial started with the presentation of the fixation stimulus, composed of two horizontal line segments. Participants were asked to fixate the empty space between them (Frame 1). After a random fixation period of 200 to 900 ms, these lines disappeared and participants had 1 s to make a saccade to a vertical line target presented between 13.38° and 14.62° eccentricity (Frame 2). As soon as the saccade was detected (in flight, Frame 3), the postsaccadic stimulus (whose contrast was adapted) was shown for 45 ms (Frame 4). This stimulus was visible for a median duration of 12 ms after saccade landing. Then participants were required to make a judgment about their postsaccadic percept via a key press (Frame 5). They had four answer options, represented in the bottom right corner. Red dots represent gaze position. Inset: spatial arrangement of the presaccadic vertical line (whose equiprobable positions are indicated by dashed lines) with respect to the horizontal postsaccadic lines.

advertisement through the French Réseau d'Information sur les Sciences Cognitives (RISC) that maintains a subject database. They had normal or corrected-to-normal vision. All were naïve as to the purpose of the study. They were not told that the pre- and post-saccadic stimuli would never be physically present at the same time on the screen. They came to the laboratory for six daily 1-hr sessions and received 10 Euros per hour. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee. Participants gave informed written consent prior to the experiment.

Stimuli and experimental design

Stimuli, generated using the Psychophysics Toolbox extensions for MATLAB (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007), were displayed on a gray background with a mean luminance of 6.30 cd/m^2 .

They were projected on a screen ($1375 \times 770 \text{ mm}$) by a digital micromirror video projector (Texas Instruments DLP 4500, VPixx Technologies, 500 Hz, Saint-Bruno, Quebec, Canada) that had a fall time for light to dark transitions and a rise time for dark to light of about 1 ns. Participants were seated in a room lighted only by the projected image, and their heads were stabilized by a chin and forehead rest at 185 cm from the screen.

Participants performed two successive phases. In the first one, we used an adaptive staircase procedure (Cornsweet, 1962) to determine the best postsaccadic stimulus contrast for reporting a fusion response. The second phase was a test with the contrast of the postsaccadic stimulus adjusted individually. These phases are explained in detail after the description of the trials.

In both phases each trial started with the presentation of two horizontal line segments ($0.05^\circ \times 0.05^\circ$) separated by 1.5° (Figure 1, frame 1). These black lines were located 7° to the right or left from screen center, with a pseudorandom vertical offset of -1° , 0° , or 1° . Participants had to fixate the empty space between these lines (to avoid retinal persistence) for a random period of 200–900 ms. Then this fixation stimulus disappeared and a vertical line ($1.4^\circ \times 0.18^\circ$) was displayed at the other side of the screen, offset on average 14° horizontally from fixation location (Figure 1, frame 2). Participants had 1 s to make a saccade to the target (a latency $>1 \text{ s}$ aborted the current trial and triggered the instruction to speed up movement initiation). When the eye crossed a 1.5° boundary around the fixation location (Figure 1, frame 3), the vertical line disappeared and was replaced with three horizontal lines (0.18° thickness) flashed for 45 ms (Figure 1, frame 4). The length of the central line was 1.24° ; it was flanked by two 0.83° lines. The center of gravity of this stimulus was always situated at 14° from the fixation location whereas the presaccadic line offset from this center was varied pseudorandomly by -0.62° , -0.32° , 0° , 0.32° , or 0.62° (inset in Figure 1). After the saccade (Figure 1, frame 5), participants were required to answer the following question: “Where did you see the vertical line at the end of your eye movement?” via a key press. Critically, they had four answer options. A response was considered as a fusion report if participants saw “the vertical line concurrently with the horizontal ones.” In this case, they had to judge whether the vertical line was situated on the right or left from the center of the postsaccadic stimulus. They could also report seeing “the horizontal lines succeeding the vertical one that had disappeared;” this was counted as a succession response. The last option (“No lines” response) corresponded with the absence of horizontal lines perceived at saccade landing.

In the first contrast adjustment phase, three independent staircases (Figure 2A) with different initial

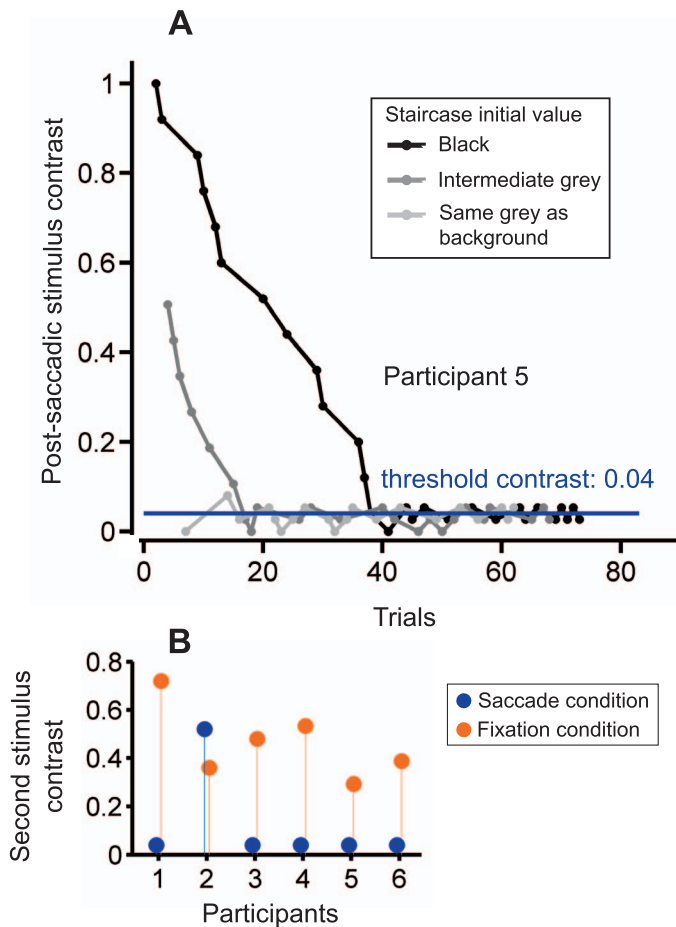


Figure 2. Adaptive staircase procedure. (A) Example of the three embedded, independent staircases (with different initial values of the post-saccadic stimulus contrast) for Participant 5 in the saccade condition. A “Succession” report lowered the next postsaccadic stimulus contrast whereas a “No lines” report elevated it. A “Fusion” report left this value unchanged. (B) Individual threshold contrasts of the second stimulus obtained in the staircase procedure of the saccade and fixation conditions.

contrast values of postsaccadic stimulus (0, 0.5, or 1) were randomly interleaved. The staircases were stopped after 15 reversals, but the whole staircase procedure could not exceed 240 trials. After a report of stimuli succession, the contrast of postsaccadic stimulus was reduced for the next trial. It was increased after a “No lines” response. A fusion report left the contrast unchanged. Figure 2A presents an example of this adaptive procedure for one participant. Individual threshold contrasts were obtained by computing the mean of the three staircases’ threshold values (which corresponded with the mean of their respective last five reversals). For five of six participants the staircases converged on a very low threshold (Figure 2B, blue circles). These individual threshold values (luminance between 1.44 and 4.70 cd/m^2) were then used to set the

contrast of the postsaccadic stimulus in the subsequent test phase, consisting of 960 trials (eight blocks of 120 trials separated by short breaks), which counterbalanced saccade directions and the positions of the vertical line.

Participants also performed a fixation condition. The procedure was the same as in the saccade condition except that they were required to keep looking at the fixation location while the vertical and horizontal lines were displayed in succession at 14° eccentricity—as soon as the peripheral stimuli appeared, the fixation stimulus was extinguished. If the gaze crossed a 2.5° boundary around the center of the fixation stimulus, the trial was aborted. This condition started with the same adaptive staircase procedure (maximum 240 trials) as the one outlined previously (see Figure S1 for individual responses). Individual thresholds tended to be higher than in the saccade condition (Figure 2B, orange circles, luminance between 0.70 and 3.04 cd/m^2). These thresholds were then used to set the contrast of the second stimulus in all 960 subsequent test trials of the second phase.

To make the two experimental conditions comparable, the time course of fixation trials was the same as in the saccade condition except the following changes. First, the delay between the fixation stimulus offset and the vertical line was fixed for each participant and corresponded to the median saccadic latency measured in the fixation condition (175–198 ms, median 179 ms). Second, presentation of the two peripheral stimuli was separated by a delay corresponding with the median saccadic duration (54–66 ms, median 60 ms). Finally, the duration of the second stimulus was defined by the median delay between the offsets of the saccade and the postsaccadic stimulus computed in the saccade condition (6–17 ms, median 12 ms). Participants 4 and 5 performed the fixation condition before the saccade one. Consequently the aforementioned time settings were retrieved from the saccade data of participants 3 and 6, respectively.

Eye movement recording and analyses

Eye movements were recorded with a video-based eye tracker (EyeLink 1000; SR Research, Ontario, Canada) and were sampled at 1000 Hz. For offline analysis, we used the EyeLink parser to identify saccades’ onset and offset, using $30^\circ/\text{s}$ velocity and $8000^\circ/\text{s}^2$ acceleration thresholds. Saccades landing 4° further from the target or the movements too slow to land before the postsaccadic stimulus offset (overall, in 8.86% of trials, $SEM = 2.03$) were discarded from the analysis.

All statistical analyses were based only on the test phases. In the saccade condition the influence of eye

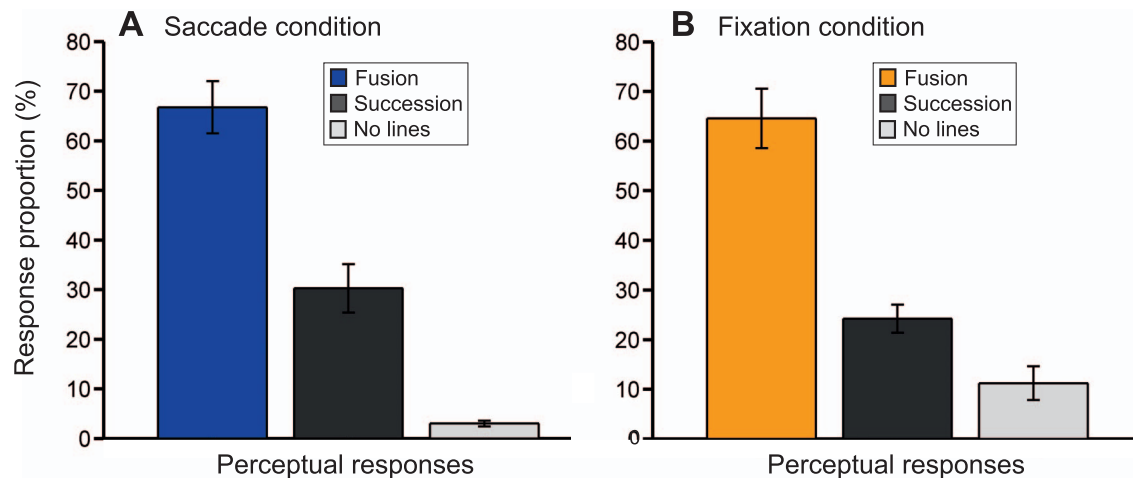


Figure 3. Response distributions. Significant reports of trans-saccadic fusion are seen in the overall response distributions averaged over the six participants in the tests with the contrast of the horizontal lines set to each participant’s threshold (obtained in the staircase procedures). (A) Saccade condition. Error bars: 1 SEM. (B) Fixation condition. Error bars: 1 SEM.

landing position on fusion responses was assessed by computing the horizontal distance between saccade endpoints and the center of the postsaccadic stimulus. Saccade endpoints were corrected by the calibration offsets reported by the Eyelink after each 5-point calibration procedure (which was implemented at the beginning of each trial block and then after a subject initiated a break or if fixation was not detected at the beginning of the trial). To isolate the effect of landing position from the influence of saccade direction, for each subject individually, the distance between saccade endpoints and the center of the postsaccadic stimulus were subtracted (hypometric saccades) or added (hypermetric saccades) to the target eccentricity (14°), and then normalized by the mean left saccade amplitude for leftward saccades and mean right saccade amplitude for rightward saccades.

To compare the proportion of perceptual responses (i.e., fusion, succession, or no line responses), we used t tests as well as 95% confidence intervals for individual response proportions. We tested the statistical significance of three fixed effect predictors—vertical line position, eye landing position, and saccade direction—on fusion responses (i.e., localization of the presaccadic stimulus on the left or right of the horizontal lines) by fitting a generalized mixed-effects model with a logistic as a link function and the localization judgment (left vs. right) as dependent variables; participant was included as random effect factor. We used the lme4 library (Bates & Sarkar, 2007), available for the open-source software R (R core team, 2015). We compared the change in the log likelihood between the full and a reduced model (i.e., without the selected predictor) using a log likelihood ratio test. We performed separate analyses in the saccade and fixation conditions, given that there was no factor of landing position in the later

(see Tables S1 and S2). A significance criterion of 0.05 was used for all statistical tests.

Results

In the saccade condition, eye movements had an average amplitude of 12.97° ($SEM = 0.28$) and an average latency of 208 ms ($SEM = 10.94$). Fusion reports were observed in 67% ($SEM = 8.84$) of trials on average, over all participants (Figure 3A). Similarly, in the fixation condition, participants reported seeing a fused percept on 65% ($SEM = 10.07$) of trials on average (Figure 3B). These proportions were significantly greater than zero, $t(5) = 5.551$, $p < 0.001$, and $t(5) = 6.412$, $p = 0.001$, respectively, but not different from each other, $t(5) = 0.309$, $p = 0.770$. This robust evidence for transsaccadic fusion was also observed individually for each participant in both experimental conditions, as indicated by the individual 95% confidence intervals (see Figure S2).

To get a larger view of the effect of the contrast of the second stimulus on the three responses, we took the response proportions in the initial contrast adjustment phase and plotted these proportions (circles in Figure 4) along with the proportions in the test phase (which were all done at the threshold contrast, squared symbols in Figure 4). We set four bins for the staircase contrasts of the adjustment phase, normalized to each participant’s final threshold [namely: ($0 - 1 \times$ threshold); ($1 - 3 \times$ threshold); ($3 - 9 \times$ threshold); (all values $\geq 9 \times$ threshold)] and computed the proportion of the three responses for each bin and these were then averaged over all the participants. As expected, the frequency of the “no horizontal lines” response

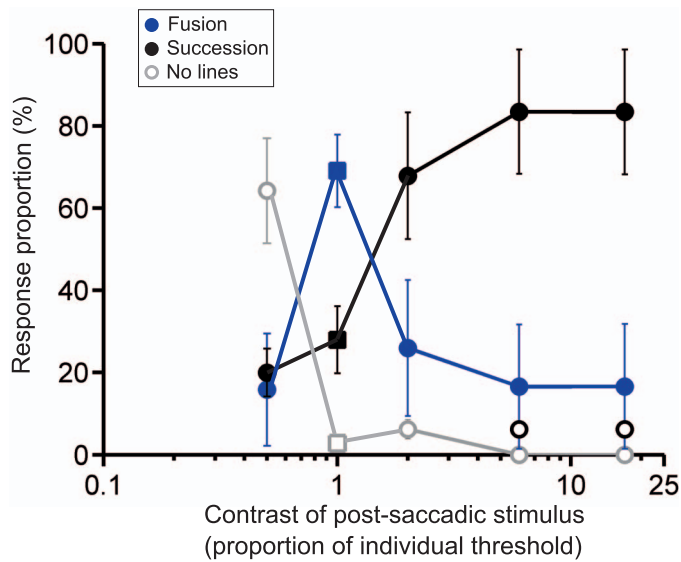


Figure 4. Response distribution (mean percentage over the six participants) as a function of the normalized contrast of the postsaccadic stimulus (divided by the final threshold contrast for each participant). Circles: data from the contrast adjustment phase. X coordinates are the centers of the following bins: (0 – 1 × threshold); (1 – 3 × threshold); (3 – 9 × threshold); (all values ≥ 9 × threshold). Squares: results of the test phase (all trials done at the threshold contrast). Error bars: 1 SEM.

decreased as their contrast increased whereas the “succession” responses increased (the horizontal lines have to be seen to support a judgement of successive stimuli). Critically, the frequency of integration responses peaked at threshold (1 on the x axis) and then dropped at higher contrasts. This indicates that the three horizontal lines suppressed the fusion of the pre- and postsaccadic images when their contrast was too high probably by masking the remapped postsaccadic representation of the vertical bar.

We then analyzed the position responses that participants gave whenever they reported fusion in the test phase using a generalized mixed-effects model separately for the saccade and fixation condition data (see Tables S1 and S2).

There was no effect of the actual position of the vertical line (with respect to the center of the postsaccadic stimulus) on its reported position in either the saccade condition [$X^2(38) = 17.44, p = 0.998$] or the fixation condition [$X^2(8) = 9.682, p = 0.288$].

Instead, in the saccade condition, the reported location of the vertical line was strongly biased by the saccade direction: The vertical line was almost always seen to the left of the horizontal lines after a saccade to the left (95% “left” responses, $SEM = 1.33$) and mostly to the right following a saccade to the right (74% “right” responses, $SEM = 13.31$), as indicated in Figure 5A [$X^2(17) = 2816.9, p \ll 0.001$]. For the fixation condition, there was no systematic difference in

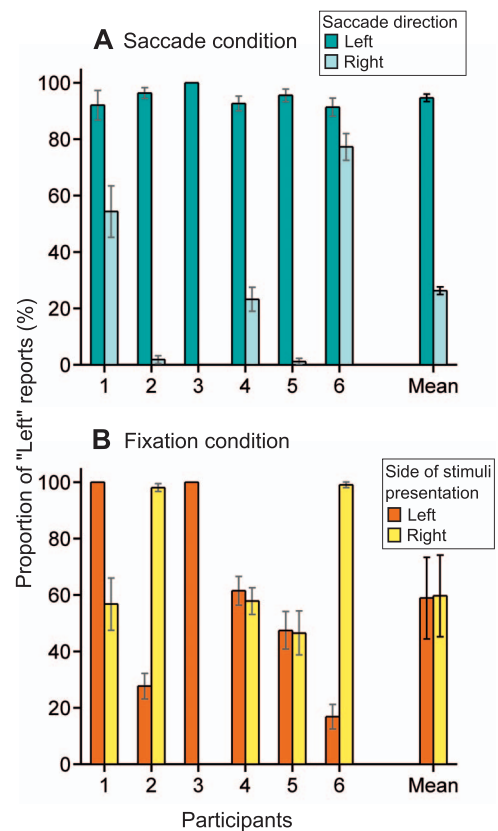


Figure 5. Location reports for vertical line relative to the center of the horizontal lines for the fusion responses. (A) Proportion of “Left” reports for leftward and rightward saccades for each participant in the saccade condition. (B) Proportion of “Left” reports when stimuli were presented on the left or right from the fixation location for each participant in the test of the fixation condition. Gray error bars for each participant show 95% confidence intervals and for the mean, black error bars show 1 SEM.

location responses for stimuli on the left compared with stimuli on the right of fixation [$X^2(5) = 9.143, p = 0.104$, see Figure 5B].

The strong bias in the location reports for three of the participants (2, 3, and 5) may have masked any effects of the offsets of the vertical line with respect to the center of the horizontal lines. So we repeated the analysis for the three participants who did have a mix of left and right responses. Again there was no effect of physical offset [$X^2(38) = 18.341, p = 0.997$] although with only three participants, the power of the analysis was low.

Finally, in the saccade condition, we assessed the effect of saccade landing position on location reports. To isolate this factor from the influence of saccade direction, we normalized the left and right landing positions by the average left and right landings for each subject individually. We found no influence of the landing position on the location reports [$X^2(17) =$

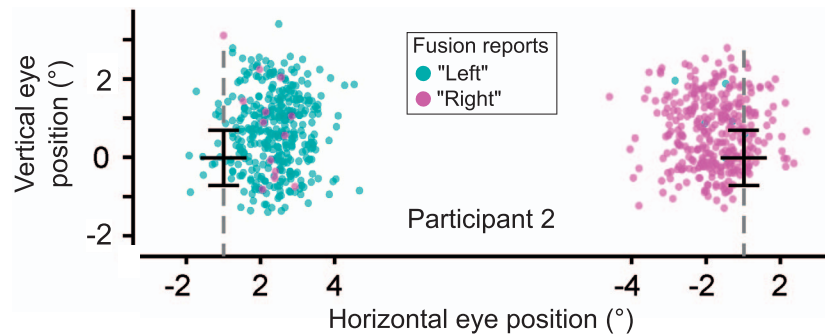


Figure 6. Perceived location of the vertical line with respect to the center of the postsaccadic stimulus as a function of the eye landing position for one participant. Each point represents one saccade.

24.887, $p = 0.097$], as illustrated in Figure 6 for one participant. Although the effect of the bias is overwhelming, there was a wide range of saccade landings including beyond the center of the horizontal bars (39% on average over the six participants), and the response proportions did not show any systematic change across this range of landings.

Discussion

Our study demonstrates that participants report that two simple, different stimuli presented across a saccade can be seen as a new, fused percept. This is the first report of transsaccadic perceptual fusion with highly dissimilar stimuli since earlier studies in the 1980s (Jonides et al., 1982; Wolf et al., 1980) that were challenged or retracted because the results were explained by monitor persistence (Irwin et al., 1983; 1990). We have no contamination from monitor persistence here for two reasons. First, our digital micromirror device had a fall and rise times for light to dark and dark to light transitions of approximately 1 ns whereas the phosphors typically used in the previous studies that reported transsaccadic fusion could be visible for hundreds of milliseconds after stimulus offset (P31 phosphor, Di Lollo, Seiffert, Burchett, Rabeeh, & Ruman, 1997; Groner, Groner, Müller, Bischof, & Di Lollo, 1993). Second, our results rule out any monitor persistence because the different locations of the presaccadic line relative to the horizontal lines had no influence on the reports of their relative locations. If the fusion effect were purely a result of display persistence, the location reports should have exactly followed the physical locations. This did not happen.

Participants reported seeing the fused percept on the majority of trials, but they also used the options of reporting a succession of the two stimuli or the absence of the postsaccadic stimulus, indicating that they differentiated between fusion and succession.

Indeed, the proportion of the three responses depended on the contrast of the second stimulus, as illustrated in Figures 2A and 4. These results also argue against the idea that responses are based on expectation of seeing fusion or on other response biases, since these biases would not vary with contrast.

This perceptual fusion was likely made possible because our task did not require the accurate alignment of the two halves of the stimulus, and second, because the second stimulus was at a lower contrast where fusion responses are more frequent (Figure 4). These two factors may explain why previous studies failed to find trans-saccadic fusion (Bridgeman & Mayer, 1983; Irwin, 1993; Irwin et al., 1983; O'Regan & Levy-Schoen, 1983; Rayner & Pollatsek, 1983). Our results confirm that pre- and postsaccadic visual percepts can be combined in spatial coordinates—in contrast, retinotopic persistence would generate a brief copy of the presaccadic image far from its original spatial location. It is highly likely that the fused percept that we report here was also present in earlier studies of feature integration across saccades (Ganmor et al., 2015; Oostwoud Wijdenes et al., 2015; Wolf & Schütz, 2015) although only by using dissimilar stimuli as we did can the perceptual nature of the integration be demonstrated.

When we compared transsaccadic fusion with fusion of stimuli presented within a single fixation (in the absence of a saccade), we found two strong similarities. First, there were similar proportions of fusion reports. We therefore propose that transsaccadic fusion is not a special case but involves the normal mode of perception, involving a general fusion mechanism that operates on sequential stimuli that appear to originate from the same location (Deubel, Koch, & Bridgeman, 2010; Germeys et al., 2010; Irwin, 1992b, 1993).

Second, in both saccade and fixation conditions, the perceived localization of the (extinguished) vertical line was mostly unaffected by the actual physical offsets of the vertical line with respect to the horizontal ones (see inset in Figure 1). This suggests

that intrinsic location information is noisy to a similar extent across a saccade and within the same fixation. This is in line with other spatially imprecise trans-saccadic phenomena such as saccadic suppression of displacement (Bridgeman, Hendry, & Stark, 1975) and compression of visual space (Ross, Morrone, Goldberg, & Burr, 2001).

If the transsaccadic fusion observed here is the expression of a general fusion mechanism, the saccade condition requires a supplementary mechanism, which is the alignment of the two targets with different retinal locations onto the same spatiotopic location. A remapping process (Duhamel, Colby, & Goldberg, 1992; but see also Zirnsak & Moore, 2014; and Neupane, Guitton, & Pack, 2016a, b) might achieve this task, carrying a representation of the presaccadic stimulus approximately into register with its original location where it is briefly available for combination with the postsaccadic stimulus. The strong directional biases that we observed argue in favor of this idea and suggest that the efference copy that allows the spatiotopic realignment is imperfect (i.e., has a gain < 1). Indeed, since saccades typically land short of the target, the predicted location of the target after the saccade is farther out than the landing position (as illustrated in Figure 7A), but this need not bias responses if the undershoot is represented in the efference copy (Collins, Rolfs, Deubel, & Cavanagh, 2009). If in addition to saccadic undershoot the efference copy itself is also hypometric (underestimates the saccade amplitude, see Figure 7B), the predicted location of the presaccadic target is then even farther out, and is thus shifted in the direction of the saccade when compared with the postsaccadic stimulus. Based on the physical undershoot that we observed, and the variability in saccade landing positions, we estimate that the efference copy gain that can explain our results would be about 0.8. This is a speculative proposal given the number of factors that interact in complex ways to produce the corrections and calibrations of saccades and the post-saccadic locations of targets. Nevertheless, earlier studies have suggested that the visual system maintains a deliberate hypometria (Harris, 1995; Havermann & Lappe, 2010; Henson, 1978; Robinson, Noto, & Bevans, 2003; Wong & Shelhamer, 2011). Hypothetically such a persistent hypometria might be reflected in efference copy. Interestingly the existence of efference copy that underestimates the saccade vector has already been assumed by others (Deubel et al., 2010; Grüsser, Krizic, & Weiss, 1987; Ostendorf, Liebermann, & Ploner, 2013; Wexler & Collins, 2014). To date the reason for this possible hypometria in both the saccade and the efference copy is unknown and beyond the scope of this study.

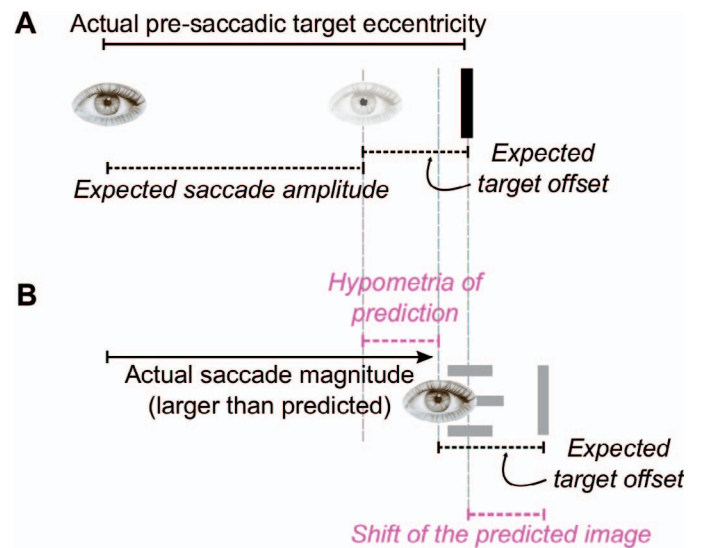


Figure 7. Schematic illustration of the hypometric efference copy explanation for the systematic directional biases observed in the saccade condition. (A) Participants prepare a rightward saccade to a vertical line. Based on the actual target eccentricity and the expected saccade magnitude, the visual system predicts the offset between the postsaccadic target and the landing position. (B) If the actual saccade magnitude is larger than expected (hypometric efference copy), i.e., the eye would land closer to the vertical line's original location, that would shift the prediction of this vertical line's location to the right of its actual presaccadic location. This would give rise to a composite percept with the vertical line situated on the right of the flashed postsaccadic stimulus.

The initial attempts to measure fusion were motivated by the belief that fusion could underlie visual stability. However, even though we now report transsaccadic perceptual fusion, our results argue against its role in this phenomenon. In particular, to observe fusion, we had to carefully adjust stimulus timing and contrast and present only these simple line stimuli—conditions very different from natural vision. Nevertheless, we were able to measure a predictive signal about the visual attributes of the saccade target that occurs during remapping. This may be related to the landmark theory of visual stability proposed by Deubel and colleagues (Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 2002) although this remains to be demonstrated. Whatever the role of the fusion in visual stability, our finding does indicate that remapping is not limited to assigning locations but can also guide the construction of composite percepts from information that is expected to be present. Possibly the remapped location pointer (Cavanagh, Hunt, Afraz, & Rolfs, 2010) is linked to the target's identity information so that it can be retrieved and instantiated at the remapped location.

Conclusion

The evidence in the 1980s against transsaccadic perceptual fusion put an end to research in this area and oriented subsequent studies toward the examination of transsaccadic memory processes (Ganmor et al., 2015; Henderson, 2008; Higgins & Rayner, 2014; Oostwoud Wijdenes et al., 2015; Wolf & Schütz, 2015). However, by simplifying the stimuli and reducing postsaccadic stimulus contrast, we showed that highly dissimilar pre- and postsaccadic visual stimuli, despite different retinal coordinates, can be combined into a single, composite percept. The formation of this new percept confirms the existence of spatiotopic persistence. Such carryover of content across saccades might constitute one of the behavioral correlates of the predictions made by the visual system.

Keywords: transsaccadic perception, spatiotopic fusion, saccades, remapping

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