Trans-saccadic integration of orientation information

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Does visual processing start anew after each eye movement, or is information integrated across saccades? Here we test a strong prediction of the integration hypothesis: that information acquired after a saccade interferes with the perception of images acquired before the saccade. We investigate perception of a basic visual feature, grating orientation, and we take advantage of a delayed interference phenomenon—in human participants, the reported orientation of a target grating, briefly presented at an eccentric location, is strongly biased toward the orientation of flanker gratings that are flashed shortly after the target. Crucially, we find that the effect is the same whether or not a saccade is made during the delay interval even though the eye movement produces a large retinotopic separation between target and flankers. However, the trans-saccadic effect nearly vanishes when flankers are displaced to a different screen location even when this location matches the retinotopic coordinates of the target. We conclude that information about grating orientation is integrated across saccades within a spatial region that is defined in external coordinates and thereby is stable in spite of the movement of the eyes.

Introduction

Despite the fact that we make frequent eye movements displacing objects onto the retina, our vision is stable and seamless. How can this feat be achieved? One possibility is that, at each eye movement, information is pooled from different retinotopic locations (Burr & Morrone, 2011; Melcher, 2007; Melcher & Colby, 2008) in order to accumulate information in the same region of external space. Consistent with this idea, "remapping" neurons have been observed to predictively shift their receptive field around the time of saccades, starting to respond to stimuli presented in the position that they will occupy after the saccade itself (Wurtz, 2008). This predictive remapping would create a period of transient spatiotopic (or at least craniotopic) integration, which could potentially support the stability of visual information across eye movements (Cicchini, Binda, Burr, & Morrone, 2013). On the other hand, an alternative possibility to the predictive remapping hypothesis is that the displacements are simply neglected and only the information necessary to guide attention and action is updated (Bridgeman, Hendry, & Stark, 1975; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Deubel & Schneider, 1996; McConkie & Currie, 1996). According to this view, visual information would be preserved in retinotopic maps while attention would be shifted across relevant or attended information across such retinotopic maps.

Several recent studies have presented evidence for trans-saccadic integration of simple visual features (Cicchini et al., 2013; Demeyer, De Graef, Wagemans, & Verfaillie, 2009; De Pisapia, Kaunitz, & Melcher, 2010; Fabius, Fracasso, & Van der Stigchel, 2016; Ganmor, Landy, & Simoncelli, 2015; Harrison & Bex, 2014; Oostwoud Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015), showing that pre-saccadic information can affect perceptual performance concerning post-saccadic stimuli. Particularly, two of these studies (De Pisapia et al., 2010; Harrison & Bex, 2014) examined the interference between stimuli presented at nearby positions (crowding) or time points (masking);

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they both found that effects in steady fixation are not completely eliminated by the execution of a saccade.

Specifically, Harrison and Bex (2014) examined release from crowding (deleterious spatial integration that impairs discriminability of a target embedded in flankers; Greenwood, Bex, & Dakin, 2009; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli & Tillman, 2008; Whitney & Levi, 2011); they found that crowding is attenuated when flankers can be previewed for some time before target presentation even if a saccade occurs during this time. This suggests that information about the flankers is carried across the saccade and across the large retinotopic distance separating the presaccadic and postsaccadic locations of the stimuli.

De Pisapia et al. (2010) examined a backward masking phenomenon (deleterious temporal integration that reduces visibility of a target followed by a mask at a similar screen position; Breitmeyer, 1984; Enns & Di Lollo, 2000); they found that some masking is still observable when a saccade is made in the interval separating target and mask even though the eye movement projects the two stimuli at remote retinotopic locations.

Moreover, Cicchini et al. (2013) measured the perceived position of flashed stimuli, usually mislocalized when occurring just before a saccade (Honda, 1989; Lappe, Atwater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997). They report that the mislocalization is virtually abolished when the probe flash is accompanied by a second flash of similar orientation and similar screen position. This stabilization effect still occurs when the second flash is presented 50–100 ms after the saccade and thereby falls at a very distant retinotopic location from the probe.

Although these three studies provide "proofs of principle" that presaccadic and postsaccadic images can interact, they give no indication of how meaningful this interaction may be—that is, compared to the transsaccadic interaction in retinotopic coordinates and to the "full" (spatiotopic and retinotopic) effect when no saccade is made—and whether presaccadic information could distort perception per se. The Harrison and Bex (2014) and the De Pisapia et al. (2010) studies tested spatiotopically matching locations and could not directly compare the strength of crowding and masking in the saccade and fixation condition due to confounding effects of suppression and mislocalization. Cicchini et al. (2013) did measure interactions over a range of positions and timings, but the quantification of the effect and their comparison with fixation were not possible because the mislocalization effect, used to probe the interaction, is itself dynamic in space-time and disappears during fixation.

In order to overcome these limitations, we designed a paradigm that combines features of the three studies above. Like in Cicchini et al. (2013), we studied the interference between stimuli that are subsequently flashed across the saccade at different spatial and temporal separations. Rather than measuring (release from) mislocalization, we measured the biases on perceived orientation provided by flanker stimuli, leveraging on the perceptual pooling occurring when several close stimuli are presented in the periphery—one of the distinctive phenomena of perceptual crowding (e.g., Greenwood et al., 2009; Harrison & Bex, 2014, Harrison & Bex, 2015; Parkes et al., 2001). Differently from what is typically done in crowding studies, however, we used briefly flashed stimuli that are separated in time—similarly to De Pisapia et al.'s (2010) study. This provided us with a tool to compare the strength of the target–flanker interaction across a saccade versus during fixation and to define the frame of reference of this interaction (spatiotopic vs. retinotopic).

Methods

Subjects

Nine subjects participated in the experiment (six females, age ranging from 24 to 28 years old). All the participants had normal or corrected-to-normal vision and provided written informed consent before taking part in the study. With the exception of one author (M.F.), they were all naive to the purpose of the experiment. All participants were tested in the saccade conditions; a subset of seven observers were also tested in a control fixation condition.

The experimental procedures were approved by the regional ethics committee [Comitato Etico Pediatrico Regionale – Azienda Ospedaliero-Universitaria Meyer – Firenze (FI)] and were in line with the declaration of Helsinki; participants gave their informed written consent upon enrollment in the study.

Apparatus

Experimental measures were performed in a quiet and dimly lit room. Stimuli were generated with a Mac Pro 4.1, running the PsychoPhysics Toolbox (Brainard, 1997; Pelli, 1997) for MATLAB (MATLAB r2010a, MathWorks, Natick, MA), and presented on a CRT monitor (Barco Calibrator Line) with a resolution of 1,024 × 768 pixels and a refresh rate of 120 Hz. Participants sat in front of the monitor screen, which subtended 40° × 30° of visual angle at a distance of 57 cm. Head position was stabilized by means of a chin and headrest, and eye movements were monitored

using the EyeLink 1000 system (SR Research, Canada) and the Eyelink toolbox for MATLAB (Cornelissen, Peters, & Palmer, 2002). The position of the left eye was measured with a frequency of 1,000 Hz by means of an infrared sensor mounted below the screen, which allowed for unrestrained viewing of the display. A standard 13-point calibration routine was performed before the beginning of each experimental session.

Stimuli

Against a uniform gray background (luminance = 37.2 cd/m^2), three stimuli were shown on each trial: one probe and two flankers. All the stimuli were oriented gratings with frequency of 2 c/deg, viewed through a circular aperture (diameter = 3°) with smoothed edges. The Michelson contrast of the gratings was 90% for the probe and 50% for the flankers. Probe orientation varied randomly between −30° and +30° around the horizontal axis; both flankers were tilted by 15° relative to the probe, either clockwise or counterclockwise. In the spatiotopic and full conditions, the flankers were aligned vertically with the probe and appeared 2.5° above and below from it. In the retinotopic condition, they still appeared above and below from the probe but were also displaced by 10° to the right so to be aligned in eye-centered coordinates. Both probe and flankers were shown for two monitor frames (17 ms); the two flankers were always shown simultaneously after the probe; the probe–flanker stimulus onset asynchrony (SOA) was variable (see Procedure).

Procedure

Trials started with observers fixating on a small spot (0.35° diameter) 5° left of center; after a variable delay (randomly varied between 500 and 800 ms), this was replaced by a similar spot located 5° right of screen center, eliciting a 10° rightward saccade (except in the control condition, in which fixation was maintained at the initial location).

At a variable time before saccadic onset, the probe was flashed (17 ms) 5° below the fixation point, followed by the two flankers (also flashed for 17 ms) with variable SOA (in different blocks of trials, the SOA was 120, 200, or 400 ms). Flankers were shown at one of two locations, also varied across blocks. In spatiotopic blocks (Figure 1A), the flankers were positioned below the fixation point, 2.5° above and below the (spatiotopic) coordinates of the probe. Alternatively, the flankers could be shown below the saccade target (Figure 1B), above and below a position corresponding to the retinotopic coordinates of the probe (when a saccade was made from the fixation point to the saccade target), or corresponding to a "neutral" position (when observers made no saccade but simply maintained their gaze on the fixation point).

At the end of each trial, a response window appeared and two judgments were collected: perceived location and perceived orientation of the probe. Using the mouse, observers first adjusted the location of a white Gaussian blob (shown with the same size and vertical location of the probe at a random horizontal location) to match the perceived position of the probe. Next, the blob turned into a grating with random orientation, and observers rotated it (moving the mouse) until it reproduced the probe orientation. Note that instructions described the flankers as task-irrelevant and encouraged observers to ignore them. In the (very rare) cases when the probe was not seen, participants clicked on the bottom-right corner of the monitor, and the trial was excluded from the analyses.

Data analysis

In an offline analysis, eye-position traces were examined to estimate the saccade onset and offset. These were defined by fitting a three-line-segment function (for details, see Binda, Morrone, Ross, & Burr, 2011).

Trials were discarded in any of the following cases: the saccade onset occurred less than 50 ms or more than 350 ms after the target onset (8.5% of trials), saccade landing deviated by more than 2° from the saccade target (17.3%), or no probe was seen (<1%). Of these, we further selected only trials in which the probe occurred between 80 and 20 ms before the saccade onset, leaving a total of 1,989 trials. In all selected trials, flankers were presented after the saccade (between 100 and 380 ms after saccade onset, depending on the SOA); i.e., probe–flanker pairs were always trans-saccadic.

Perceived probe orientation was calculated separately for the two flanker conditions (+15° and −15°; see Figure 1C and D). The response error (i.e., difference between reported and physical orientations) was normalized to the target–flanker orientation difference (either +15° or −15°), yielding an index of the flankers' effect for each individual trial. This was averaged across trials testing each condition and SOA and shown in Figures 2 and 3. We verified that conclusions hold if alternative definitions of the flankers' effect are used—for example, fitting the distribution of response errors separately for the +15° and −15° flankers (continuous lines in Figure 1C and D) and comparing the intercept of the curves.

Additionally, when comparing data obtained in the saccade conditions with the data obtained in fixation, we calculated the Bayes factor (Dienes, 2014). This

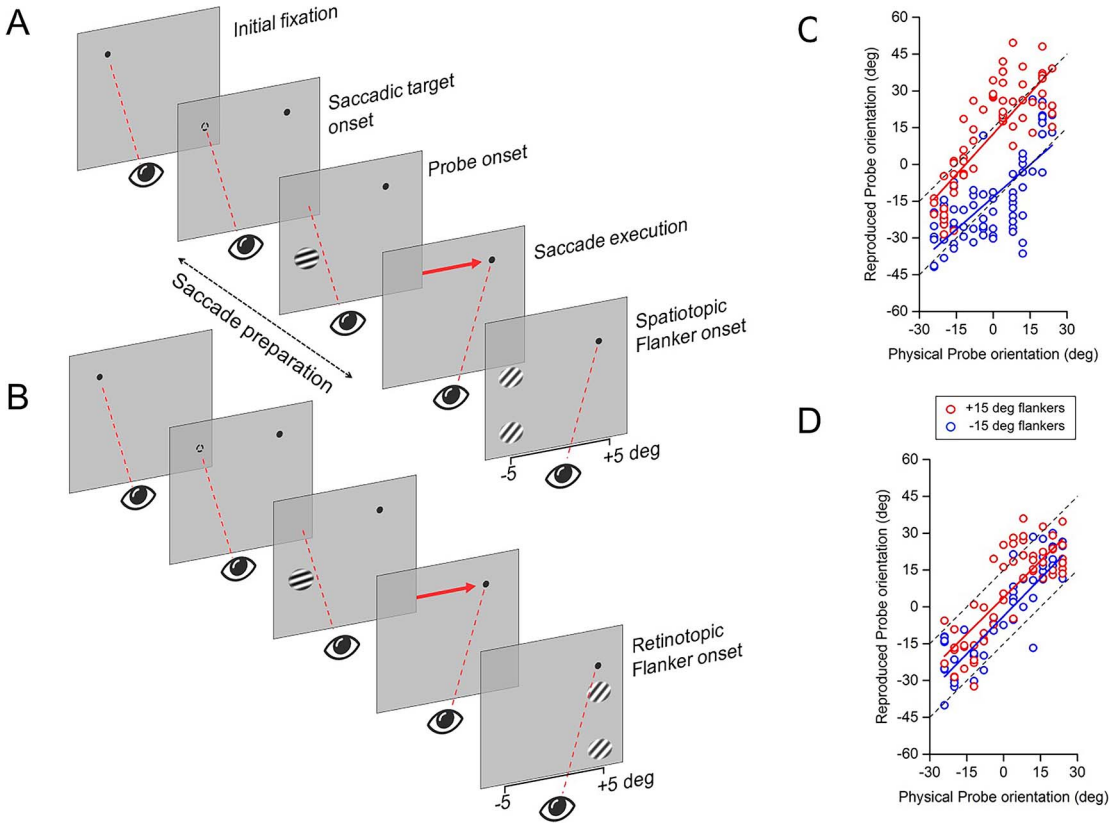

Figure 1. Experimental procedures and example data. (A–B) Stimulus sequence for trans-saccadic probe–flanker pairs. Subjects made a 10° rightward saccade (red arrow). A probe grating was flashed below the initial fixation point between 80 and 20 ms before saccade onset; after saccade completion, two similar gratings were shown above and below the spatiotopic position of the probe (A) or its retinotopic position (B). Flankers were tilted ±15° relative to the probe. Subjects reported probe orientation by manually adjusting the tilt of a response grating (not shown in figure). (C–D) Sample data from the trans-saccadic retinotopic and spatiotopic conditions. Symbols show single-trial probe orientation adjustments, plotted against the actual probe orientation. Red and blue circles are trials with flankers tilted +15° or −15° relative to the probe, respectively (dashed black lines show the flankers' orientation; continuous lines give the best linear fit across data points in each condition). The separation between red and blue points reflects the flankers' interference on perceived probe orientation: large in the spatiotopic (C) but negligible in the retinotopic condition (D).

index indicates how strongly the data supports the null hypothesis (i.e., no effect of the experimental manipulation) or the alternative hypothesis (i.e., the experimental manipulation causes a significant effect) and allows discrimination of whether a null result actually provides evidence in favor of the null hypothesis or is just lack of evidence for either hypothesis. Bayes factors smaller than 0.3333 (one third) indicate support for the null hypothesis; Bayes factors greater than three, on the other hand, indicate support for the alternative hypothesis. Conversely, values comprised between 0.3333 and three indicate that data is too weak to support either hypothesis.

Results

Our main finding is that the perceived orientation of a grating flashed before a saccade is biased toward the orientation of flanker gratings flashed after the saccade at similar screen (spatiotopic) coordinates (Figure 1A and C). This trans-saccadic effect is reduced or absent if the flankers are shown at a different screen position even if matching the retinotopic coordinates of the probe (Figure 1B and D).

Specifically, participants used the adjustment method to report the perceived orientation of the probe grating (individual symbols in Figure 1C and D); the two flankers, flashed 120 ms after the probe, could be tilted clockwise (+15°) or counterclockwise (−15°) relative to the probe; this led to a clockwise or counterclockwise bias of perceived probe orientation, respectively (blue and red in Figure 1C and D). The maximum flanker effect is a ±15° bias on the single trial (marked by the dotted lines in Figure 1C and D and normalized to one to define the "flankers' effect" shown in Figures 2 and 3). For trans-saccadic probe–flanker pairs shown at matching screen positions (aligned in spatiotopic coordinates), the biasing effect is

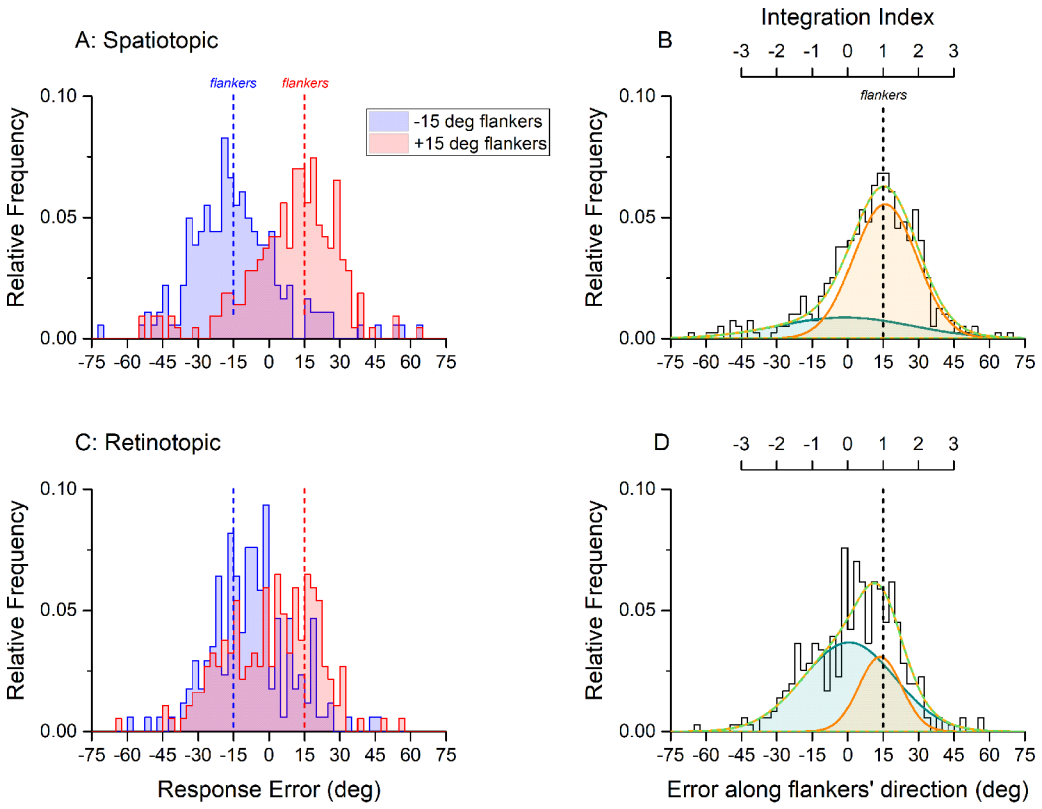

Figure 2. Error distributions for trans-saccadic crowding. (A) Distributions of orientation reproduction errors for trans-saccadic trials in which target and flankers were presented in the same spatiotopic position. Red distribution refers to trials in which the postsaccadic flankers were oriented 15° more clockwise (red dashed line); blue distribution refers to trials in which the flankers were oriented 15° counterclockwise (blue dashed line). (B) Data for the spatiotopic condition realigning clockwise and counterclockwise trials. Biases of 15° imply a full capture by the flankers and lead to an integration index of 1. Data were fit with the sum of two Gaussian distributions (green and orange). (C) Same as panel A but for flankers presented in the same retinotopic position. (D) Same as above but for the retinotopic condition.

close to maximum; however, the flankers' effect is very small for probe–flanker pairs shown at similar retinotopic coordinates (hence, distant screen positions).

In Figure 2, we plot response error distributions for the two conditions: probe–flanker pairs aligned in spatiotopic (top) or retinotopic (bottom) coordinates. Leftmost plots display orientation reproduction errors with the two flanker conditions shown in different colors (red = flankers tilted 15° clockwise, blue = 15° tilted counterclockwise relative to the probe). In the spatiotopic condition, trials with different flankers have well-separated error distributions, laying very close to the flankers' orientation (indicated by colored dashed lines). The pattern is similar for the retinotopic condition (Figure 2C), but the two distributions are less separated. We also compared the spread of the error distributions for individual participants and found them to be statistically indistinguishable: 18.7 ± 2.9 spatiotopic, 16.9 ± 1.7 retinotopic; two-way repeated measures ANOVA with factors flanker ±15° and position spatiotopic/retinotopic, main effect of position, $F(1, 8) = 1.7$, $p = 0.22$.

To gain statistical power, we collapsed data from the two flanker conditions and plot errors in the flankers' direction in Figure 2B and D. The resulting error distributions are well modeled by the weighted sum of two Gaussian random processes (orange and green lines) centered around the flankers (15°) and the probe (0°) orientation with very different weights in the spatiotopic and retinotopic conditions. We estimated these by fitting the distributions with a composite Gaussian model, in which the mean, variance, and weight of two random processes are free to vary. The spatiotopic distribution (Figure 2B) is almost entirely explained by a single Gaussian (orange distribution) centered at 15.87° ($\sigma = 13.5$, weight = 0.75) with only a minor contribution by a second random process (green distribution) centered at −1.15° with a large variance ($\sigma = 28.5$, weight = 0.25). The situation almost reverses in the case of retinotopic flankers (Figure 2D) as these responses result primarily from a Gaussian process centered close to zero (0.58°; $\sigma = 19.4$, weight = 0.72) with only a small contribution from a process centered close to the flankers (13.79°; $\sigma = 9.1$, weight = 0.28).

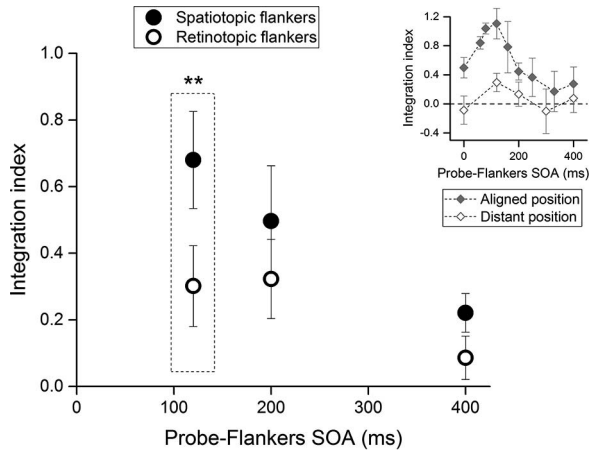

Figure 3. Flankers' effect as function of probe–flanker SOA. Average flankers' effect (defined, for each trial, as the ratio between the orientation judgment error and the flankers' tilt, which was either +15° or −15°) shown as function of the probe–flanker SOA. Main panel: data for trans-saccadic probe–flanker pairs, presented at matching spatiotopic (filled symbols) or retinotopic coordinates (empty symbols). The SOA 120 ms condition was tested on all participants ($N = 9$); the others were tested on a subset of participants (spatiotopic: $N = 6$ and 8 for SOA = 200 and 400 ms, respectively; retinotopic: $N = 6$ for both SOA = 200 and 400 ms). Inset: data from three subjects in steady fixation, in which we explored how the flankers' effect varies with SOA and position of the flankers (above and below the probe or displaced by 10° rightward at the same screen position used for the "retinotopic" flankers of the trans-saccadic trials). In all cases, error bars show *SEM* across participants. $^{**}p < 0.01$.

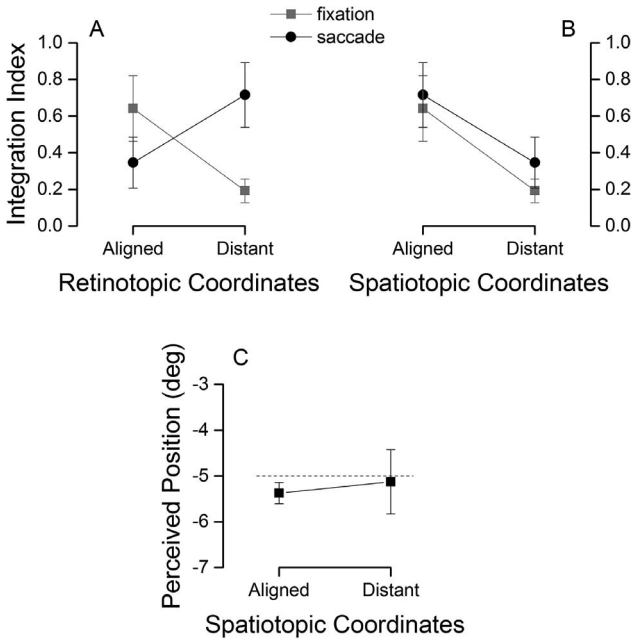

Figure 4. Trans-saccadic versus fixation conditions. The top panels show the same average flankers' effect plotted either as function of the probe–flanker position in retinotopic (A) or spatiotopic coordinates (B), separately for trans-saccadic probe–flanker pairs and for pairs presented in steady fixation (see legend). (C) Perceived probe position (with the dashed line marking the veridical position) with the same conventions as in panel B, i.e., as function of the spatiotopic spatial relationship between probe and flankers. Error bars show *SEM* across participants with $N = 7$ in all cases.

To summarize the tendency to produce errors in the direction of the flankers, we computed an "integration index" (obtained by normalizing errors by the flankers-to-probe orientation difference, shown at the top of Figure 2B and D). This value was averaged across trials of each participant, and means were compared across the several conditions we tested: varying probe–flanker spatiotemporal distance.

Figure 3 (main panel) shows the integration index as function of the probe–flanker temporal distance (SOA). We find that, for trans-saccadic probe–flanker pairs, the effect is significantly stronger for spatiotopic than retinotopic matches at SOA 120 ms (paired t test), $t(8) = 3.47$, $p = 0.004$, while, as the effect decreases with increasing probe–flanker SOA, the difference between spatiotopic and retinotopic flankers resulted to be weaker, $t(5) = 0.92$, $p = 0.20$ and $t(6) = 1.48$, $p = 0.09$, respectively, for spatiotiopic versus retinotopic flankers at 200 ms and 400 ms SOA.

The flankers' effect tapers off with longer SOAs, yet the spatiotopic effect remains significant at all the SOAs tested (one-sample t test), $t(8) = 4.95$, $p = 0.024$; $t(5) = 3.28$, $p = 0.011$; and $t(7) = 4.10$, $p = 0.002$, respectively, for 120, 200, and 400 ms. The tendency for the flankers' effect to decrease at longer SOAs is observed in steady fixation as well (inset). In this condition, we explored a larger range of SOAs in three subjects; the results show that the flankers' effect is larger at 120 ms than for simultaneous probe–flanker pairs, and it decreases thereafter. They also show that the flankers' effect is spatially specific, being weaker for flankers displaced by 10° away from the probe although showing significant effects with SOAs of 120 and 200 ms (one-sample t tests), $t(8) = 2.63$, $p = 0.015$; $t(5) = 2.97$, $p = 0.016$; $t(5) = 1.43$, $p = 0.10$, respectively, for 120, 200, and 400 ms. This is important because 10° is also the (retinotopic) distance of trans-saccadic probe and flanker pairs aligned in spatiotopic coordinates—where the effect is strong. This observation suggests that spatiotopic, not retinotopic, distance is the key variable that determines the strength of the flanker–probe interaction.

In order to test directly for this possibility, Figure 4A and B compares the two main trans-saccadic conditions (SOA 120 ms, spatiotopic alignment, implying a 10° retinotopic separation, vs. retinotopic alignment, implying a 10° spatiotopic separation) with two steady-

fixation conditions (SOA 120 ms, spatiotopic + retinotopic alignment vs. a neutral position with 10° separation) that were tested on a subset of our subjects (seven out of nine). Figure 4A plots the results in retinotopic coordinates, showing a strong interaction between the two factors: saccade (yes/no) and retinotopic probe–flanker coordinates (aligned/distant, corresponding to 0°/10° retinotopic separation). This is supported by a two-way repeated-measures ANOVA, revealing a significant interaction between the two factors, $F(2, 6) = 15.3$, $p = 0.008$, but no main effects, $F(1, 6) = 1.85$, $p = 0.22$ and $F(1, 6) = 0.22$, $p = 0.66$, respectively, for the saccade and probe–flanker coordinates factor, and implying that the probe–flanker proximity in retinotopic coordinates is irrelevant for determining their interaction. Post hoc tests further support this interpretation, showing that (a) the trans-saccadic spatiotopic effect is as strong as the "full" effect (paired t test), $t(6) = -0.52$, $p = 0.62$, Bayes factor $= 0.298$, measured in steady fixation with stimuli aligned in both spatiotopic and retinotopic coordinates; and (b) the trans-saccadic retinotopic effect is the same as the effect of flankers located at a neutral location away from the probe (distant flankers, in steady fixation; paired t test), $t(6) = 1.7$, $p = 0.15$, Bayes factor $= 0.114$, meaning that the retinotopic effect is explained out by a nonspatially specific component of the effect. This analysis also confirms the results in Figure 3 showing that the trans-saccadic spatiotopic effect is reliably larger than the retinotopic one (paired t test), $t(6) = 2.7$, $p = 0.019$.

Finally, Figure 4B replots the same data as function of probe–flanker spatiotopic coordinates. With this rearrangement, it becomes clear that both data sets obtained in fixation and trans-saccadically are well explained by a single factor: the probe–flanker proximity in spatiotopic coordinates.

Figure 4C shows the same analysis for perceived position judgments. Probe perceived position was close to veridical in all cases even when presented perisaccadically. This lack of perisaccadic mislocalization is not surprising because probes were always shown more than 20 ms before the saccade onset while the peak of mislocalization is at or after the saccade onset (Lappe et al., 2000). Stimuli also had relatively long duration (two frames or 17 ms; studies showing strong mislocalization often used durations <10 ms). Moreover, a "position-attraction" effect of the kind reported by Cicchini et al. (2013) should contribute to veridically localizing probes paired with postsaccadic flankers at matching spatiotopic coordinates. By the same token, one expects that flankers shown at matching retinotopic coordinates (and thereby different spatiotopic positions) should "attract" the probe away from its veridical location and induce some mislocalization in the direction of the saccade as indeed suggested by the (not significant) tendency for rightward displacement in the "distant flankers" condition in Figure 4C (distant in spatiotopic coordinates, implying aligned probe–flankers in retinotopic coordinates (paired-sample t test), $t(6) = 0.43$, $p = 0.68$.

Discussion

By studying the interference of task-irrelevant postsaccadic flankers on a presaccadic probe, we gather evidence that visual information is integrated across saccades in spatiotopic coordinates. This is consistent with three recent studies providing proofs of principle that trans-saccadic integration may happen in spatiotopic coordinates, i.e., sampling information from different retinotopic locations before and after the saccade that correspond to the same screen location (Cicchini et al., 2013; De Pisapia et al., 2010; Harrison & Bex, 2014). Our data take us a significant step further, showing that spatiotopic integration is not just possible, but represents the main mode of trans-saccadic integration—at least, for the type of information probed by our task. This is supported by two pieces of evidence. First, we show that trans-saccadic spatiotopic integration is as strong as the integration in steady fixation; this means that the flanker interference effect remains unaffected even when the saccade produces a 10° retinotopic separation between probe and flankers. Second, we show that flankers located away from the spatiotopic coordinates of the probe produce very weak interference and that the location corresponding to the retinotopic coordinates of the probe is no exception; this means that interference across different screen locations remains weak even if the saccade nulls their retinotopic separation.

Several previous studies investigated which frame of reference—retinotopic or spatiotopic—is used for visual representations and often did so by using the adaptation technique. Our task involved a simple visual feature: orientation, for which earlier adaptation studies have found a primary retinotopic component (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Melcher, 2005; Zimmermann, Morrone, Fink, & Burr, 2013). However, more recent studies (He, Mo, & Fang, 2017; Nakashima & Sugita, 2017; Zimmermann, Weidner, Abdollahi, & Fink, 2016) increasingly show a spatiotopic component when measuring adaptation effects on perceived orientation, such as the tilt aftereffect. For instance, Zimmermann et al. (2016), combining behavioral and fMRI techniques, found adaptation aftereffect on orientation perception in both retinal and spatial coordinates, suggesting a transfer of orientation representations from a retinotopic to a spatiotopic reference frame. Our results, on the other hand,

highlight an almost completely spatiotopic effect, suggesting that the functional mechanisms probed by our paradigm might be different from the ones probed by adaptation, although we cannot draw any strong conclusion about the specific nature of the mechanisms probed by different techniques. Investigating whether and to what extent different paradigms probe similar functional mechanisms and neural substrates thus represents an intriguing possibility for future studies.

The paradigm we used shares key features with two phenomena: masking and crowding. Like in masking, our paradigm involves the interference between stimuli presented briefly and sequentially. Masking often impairs the visibility of the probe stimulus, typically by replacing it with a high-contrast stimulus at the same or nearby spatial location (Enns & Di Lollo, 2000). In our case, however, flankers never overlapped with the probe location, and subjects reported seeing it indicating that probe visibility was not compromised (i.e., $<1\%$ of cases in which participants reported not seeing the probe). Nevertheless, the flankers biased the perceived orientation of the probe as though nearby features are mandatorily averaged. This is particularly clear if we examine response distributions (Figure 2). At least in the spatiotopic condition, this distribution is well explained by a single Gaussian distribution centered nearby the flankers (Figure 2B), indicating a genuine integration of information.

Several lines of evidence show that perisaccadic perception is particularly degraded (Binda, Bruno, Burr, & Morrone, 2007; Crevecoeur & Kording, 2017); in such cases, it may be possible that subjects default to reproducing the flanker's orientation. However, this would predict similar effects in the spatiotopic and retinotopic conditions whereas we find integration only for the spatiotopic condition. If the tendency to default to the flankers' orientation took place only in the spatiotopic condition (presumably because probe and flankers are perceived at similar positions), one would expect very narrow distributions in the spatiotopic condition. However, we find that the variance of the error distributions was very similar in the retinotopic and spatiotopic conditions.

Our findings relate conceptually to the phenomenon of crowding (Parkes et al., 2001; Pelli & Tillman, 2008; Whitney & Levi, 2011) with the peculiarity that our stimuli are not simultaneous and steady as they typically are in this literature. Although crowding is traditionally envisaged as a retinotopic process, recent evidence suggests that alternative frames of reference operate as well (Harrison & Bex, 2014) and do not necessarily operate on retinotopic coordinates (Maus, Fischer, & Whitney, 2011). Some effect may even spread to positions far removed from the flankers when the probe–flanker configuration is visible before a saccade (Harrison et al., 2013). Crowding occurs in spite of no loss of acuity or other limitations in early visual cortex and may be conceptualized as an active filter, applied to the visual stimulus to face the overwhelming amount of information reaching the visual cortex (Maus et al., 2011). Target identification as well as selection of the information that needs filtering out might be complex processes, spanning over hundreds of milliseconds and exceeding the typical fixation duration (Cicchini et al., 2013; Cicchini & Kristjánsson, 2015; Fischer & Whitney, 2014). This would explain the existence of a mechanism that compensates for eye movements and pools over spatiotopic regions of space.

One such mechanism may be the "receptive fields remapping" observed in several brain areas around the time of saccades (Duhamel, Colby, & Goldberg, 1992). These neurons shift their receptive field in the proximity of a saccade—an observation that has been linked to a putative predictive process anticipating what the spatial position after the saccade will be. Because the same population of neurons is engaged in monitoring different retinotopic positions, this may explain the interaction among remote locations observed perisaccadically—both as "remote crowding" (Harrison et al., 2013) and as the "position attraction" among remote perisaccadic stimuli shown in Cicchini et al. (2013). Crucially, the different retinotopic positions monitored by a given remapping neuron correspond to the same screen position across the saccade (except in one study, Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014), implying that remapping can support spatiotopic integration across saccades. Although remapping has been linked to the maintenance of stable space representations across saccades (Wurtz, 2008), recently a debate has opened on the interpretation of this phenomenon and the way it may relate to visual perception (Marino & Mazer, 2016; Zirnsak et al., 2014). The possibility has been raised that no information needs transferring across retinotopic locations—objects' features might be preserved in a retinotopic map (which, like the retina itself, shifts every time the eyes move); perceptual stability may be maintained by redirecting attention to the relevant retinotopic location (Cavanagh et al., 2010). If this is the case, remapping receptive fields should carry no feature information (contrary to what shown in Subramanian & Colby, 2014). This hypothesis also suggests a predominance of retinotopic representation as the "native" coordinate system for visual perception (Golomb, Chun, & Mazer, 2008). Our data clearly speak against it, showing that, at least in this context, feature integration is predominantly spatiotopic (Figures 1 and 3) with no retinotopic effect emerging above a spatially a-specific interference effect (Figure 4).

In conclusion, our study shows that information about simple visual features (such as orientation) is

integrated across saccades. The paradigm we adopted has two key characteristics: It allows for comparing integration across saccades and during fixation and across disparate positions in the visual field. These may be exploited in future studies to map the spatial area over which trans-saccadic interactions (vs. interactions during fixation) occur. Comparing this with the spatial profile of remapping receptive fields (such as in Cicchini et al., 2013) should further our understanding of the basic visual mechanisms for perceptual stability across saccades.

Keywords: saccadic eye movements, trans-saccadic integration, visual stability, orientation perception, visual crowding

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References

Binda, P., Bruno, A., Burr, D. C., & Morrone, M. C. (2007). Fusion of visual and auditory stimuli during saccades: A Bayesian explanation for perisaccadic distortions. *Journal of Neuroscience*, *27*(32), 8525–8532, https://doi.org/10.1523/JNEUROSCI.0737-07.2007.

Binda, P., Morrone, M. C., Ross, J., & Burr, D. C. (2011). Underestimation of perceived number at the time of saccades. *Vision Research*, *51*(1), 34–42, https://doi.org/10.1016/j.visres.2010.09.028.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436, https://doi.org/10.1163/156856897X00357.

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. Oxford: Clarendon Press.

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, https://doi.org/10.1016/0042-6989(75)90290-4.

Burr, D. C., & Morrone, M. C. (2011). Spatiotopic coding and remapping in humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1564), 504–515, https://doi.org/10.1098/rstb.2010.0244.

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, https://doi.org/10.1016/j.tics.2010.01.007.

Cicchini, G. M., Binda, P., Burr, D. C., & Morrone, M. C. (2013). Transient spatiotopic integration across saccadic eye movements mediates visual stability. *Journal of Neurophysiology*, *109*(4), 1117–1125, https://doi.org/10.1152/jn.00478.2012.

Cicchini, G. M., & Kristjánsson, Á. (2015). Guest editorial: On the possibility of a unifying framework for serial dependencies. *I-Perception*, *6*(6), 1–16, https://doi.org/10.1177/2041669515614148.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers: A Journal of the Psychonomic Society, Inc.*, *34*(4), 613–617, https://doi.org/10.3758/BF03195489.

Crevecoeur, F., & Kording, K. P. (2017). Saccadic suppression as a perceptual consequence of efficient sensorimotor estimation. *eLife*, *6*: e25073, https://doi.org/10.7554/eLife.25073.

Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2009). Transsaccadic identification of highly similar artificial shapes. *Journal of Vision*, *9*(4):28, 1–14, https://doi.org/10.1167/9.4.28. [PubMed] [Article]

De Pisapia, N., Kaunitz, L., & Melcher, D. (2010). Backward masking and unmasking across saccadic eye movements. *Current Biology*, *20*(7), 613–617, https://doi.org/10.1016/j.cub.2010.01.056.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837, https://doi.org/10.1016/0042-6989(95)00294-4.

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, *5*(July), 1–17, https://doi.org/10.3389/fpsyg.2014.00781.

Duhamel, J. R., Colby, C., & Goldberg, M. (1992,

January 3). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*(5040), 90–92, https://doi.org/10.1126/science.1553535.

Enns, J., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Sciences*, *4*(9), 345–352, https://doi.org/10.1016/S1364-6613(00)01520-5.

Fabius, J. H., Fracasso, A., & Van der Stigchel, S. (2016). Spatiotopic updating facilitates perception immediately after saccades. *Scientific Reports*, *6*: e34488, https://doi.org/10.1038/srep34488.

Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience*, *17*(5), 738–743, https://doi.org/10.1038/nn.3689.

Ganmor, E., Landy, M. S., & Simoncelli, E. P. (2015). Near-optimal integration of orientation information across saccades. *Journal of Vision*, *15*(16):8, 1–12, https://doi.org/10.1167/15.16.8. [PubMed] [Article]

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The native coordinate system of spatial attention is retinotopic. *Journal of Neuroscience*, *28*(42), 10654–10662, https://doi.org/10.1523/JNEUROSCI.2525-08.2008.

Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2009). Positional averaging explains crowding with letter-like stimuli. *Proceedings of the National Academy of Sciences, USA*, *106*(31), 13130–13135, https://doi.org/10.1073/pnas.0901352106.

Harrison, W. J., & Bex, P. J. (2014). Integrating retinotopic features in spatiotopic coordinates. *Journal of Neuroscience*, *34*(21), 7351–7360, https://doi.org/10.1523/JNEUROSCI.5252-13.2014.

Harrison, W. J., & Bex, P. J. (2015). A unifying model of orientation crowding in peripheral vision. *Current Biology*, *25*(24), 3213–3219, https://doi.org/10.1016/j.cub.2015.10.052.

Harrison, W. J., Retell, J. D., Remington, R. W., & Mattingley, J. B. (2013). Visual crowding at a distance during predictive remapping. *Current Biology*, *23*(9), 793–798, https://doi.org/10.1016/j.cub.2013.03.050.

He, D., Mo, C., & Fang, F. (2017). Predictive feature remapping before saccadic eye movements. *Journal of Vision*, *17*(5):14, 1–12, https://doi.org/10.1167/17.5.14. [PubMed] [Article]

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics*, *45*(2), 162–174, https://doi.org/10.3758/BF03208051.

Knapen, T., Rolfs, M., Wexler, M., & Cavanagh, P. (2010). The reference frame of the tilt aftereffect. *Journal of Vision*, *10*(1):8, 1–13, https://doi.org/10.1167/10.1.8. [PubMed] [Article]

Lappe, M., Awater, H., & Krekelberg, B. (2000, February 24). Postsaccadic visual references generate presaccadic compression of space. *Nature*, *403*(6772), 892–895, https://doi.org/10.1038/35002588.

Marino, A. C., & Mazer, J. A. (2016). Perisaccadic updating of visual representations and attentional states: Linking behavior and neurophysiology. *Frontiers in Systems Neuroscience*, *10*: e3, https://doi.org/10.3389/fnsys.2016.00003.

Maus, G. W., Fischer, J., & Whitney, D. (2011). Perceived positions determine crowding. *PLoS One*, *6*(5): e19796, https://doi.org/10.1371/journal.pone.0019796.

McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*(3), 563–581, https://doi.org/10.1037/0096-1523.22.3.563.

Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Current Biology*, *15*(19), 1745–1748, https://doi.org/10.1016/j.cub.2005.08.044.

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10*(7), 903–907, https://doi.org/10.1038/nn1917.

Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*(12), 466–473, https://doi.org/10.1016/j.tics.2008.09.003.

Nakashima, Y., & Sugita, Y. (2017). The reference frame of the tilt aftereffect measured by differential Pavlovian conditioning. *Scientific Reports*, *7*: e40525, https://doi.org/10.1038/srep40525.

Oostwoud Wijdenes, L., Marshall, L., & Bays, P. M. (2015). Evidence for optimal integration of visual feature representations across saccades. *Journal of Neuroscience*, *35*(28), 10146–10153, https://doi.org/10.1523/JNEUROSCI.1040-15.2015.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, *4*(7), 739–744, https://doi.org/10.1038/89532.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442, https://doi.org/10.1163/156856897X00366.

Pelli, D. G., & Tillman, K. A. (2008). The uncrowded

window of object recognition. *Nature Neuroscience,* 1129–1135, https://doi.org/10.1038/nn.2187.

Ross, J., Morrone, M. C., & Burr, D. C. (1997, April 10). Compression of visual space before saccades. *Nature*, *386*(6625), 598–601, https://doi.org/10.1038/386598a0.

Subramanian, J., & Colby, C. L. (2014). Shape selectivity and remapping in dorsal stream visual area LIP. *Journal of Neurophysiology*, *111*(3), 613–627, https://doi.org/10.1152/jn.00841.2011.

Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160–168, https://doi.org/10.1016/j.tics.2011.02.005.

Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, *15*(16):1, 1–18, https://doi.org/10.1167/15.16.1. [PubMed] [Article]

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089, https://doi.org/10.1016/j.visres.2008.03.021.

Zimmermann, E., Morrone, M. C., Fink, G. R., & Burr, D. (2013). Spatiotopic neural representations develop slowly across saccades. *Current Biology*, *23*(5), https://doi.org/10.1016/j.cub.2013.01.065.

Zimmermann, E., Weidner, R., Abdollahi, R. O., & Fink, G. R. (2016). Spatiotopic adaptation in visual areas. *Journal of Neuroscience*, *36*(37), 9526–9534, https://doi.org/10.1523/JNEUROSCI.0052-16.2016.

Zirnsak, M., Steinmetz, N. A., Noudoost, B., Xu, K. Z., & Moore, T. (2014, March 27). Visual space is compressed in prefrontal cortex before eye movements. *Nature*, *507*(7493), 504–507, https://doi.org/10.1038/nature13149.