

Feature integration is unaffected by saccade landing point, even when saccades land outside of the range of regular oculomotor variance

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The experience of our visual surroundings appears continuous, contradicting the erratic nature of visual processing due to saccades. A possible way the visual system can construct a continuous experience is by integrating presaccadic and postsaccadic visual input. However, saccades rarely land exactly at the intended location. Feature integration would therefore need to be robust against variations in saccade execution to facilitate visual continuity. In the current study, observers reported a feature (color) of the saccade target, which occasionally changed slightly during the saccade. In transsaccadic change-trials, observers reported a mixture of the pre- and postsaccadic color, indicating transsaccadic feature integration. Saccade landing distance was not a significant predictor of the reported color. Next, to investigate the influence of more extreme deviations of saccade landing point on color reports, we used a global effect paradigm in a second experiment. In global effect trials, a distractor appeared together with the saccade target, causing most saccades to land in between the saccade target and the distractor. Strikingly, even when saccades land further away (up to 4°) from the saccade target than one would expect under single target conditions, there was no effect of saccade landing point on the reported color. We reason that saccade landing point does not affect feature integration, due to dissociation between the intended saccade target and the actual saccade landing point. Transsaccadic feature integration seems to be a mechanism that is dependent on visual spatial attention, and, as a result, is robust against variance in saccade landing point.

Introduction

We experience that visual perception is continuous, contradicting the disruptions of visual processing due to eye-movements (saccades). This lack of insight into the disruptive nature of saccades (Burr, Morrone, & Ross, 1994; Deubel, Schneider, & Bridgeman, 1996; Matin, 1974), allowing us to perceive the visual world as a continuous whole rather than disparate snapshots, is one of the more complex qualities of the visual system. One of the proposed mechanisms to bridge the gap in visual processing before and after a saccade is transsaccadic feature integration (Herwig, 2015). Transsaccadic feature integration involves storing retinal input of the saccade target before the saccade and *combining* the stored presaccadic information with the retinal image after the saccade (Ganmor, Landy, & Simoncelli, 2015; Oostwoud Wijdenes, Marshall, & Bays, 2015; Van der Stigchel & Hollingworth, in press; Wolf & Schütz, 2015). Combining visual feature estimates in this manner allows for more reliable estimates of visual input than when only viewed before or after the saccade, and for presaccadic perception to influence postsaccadic perception. However, the influence of presaccadic perception on postsaccadic feature perception experiments is quite small (Ganmor et al., 2015; Wolf & Schütz, 2015). This limited usefulness of transsaccadic feature integration has led to contentiousness about the nature of such a process. For

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instance, both behavioral and neurophysiological studies range from evidence in favor of feature integration (e.g., He, Mo, & Fang, 2017; Wittenberg, Bremmer, & Wachtler, 2008), evidence for very limited feature integration (e.g., Subramanian & Colby, 2014), and evidence against transsaccadic feature integration (e.g., Jonides, Irwin, & Yantis, 1983; Morris et al., 2010). Proponents of feature integration have suggested that visual continuity may be the product of a match (or lack of conflict) between pre- and postsaccadic retinal input, allowing the visual system to assume that information was present continuously (Herwig, 2015). Although this seems like an elegant solution of how the visual system may establish perceptual continuity across saccades, little is known about how and whether transsaccadic feature integration is affected by the parameters of a saccade. As of yet, no consensus exists whether transsaccadic feature integration is a higher-order process (Hübner & Schütz, 2017) or a lower order visual process (Paeye, Collins, & Cavanagh, 2017). Therefore, we chose to approach the topic of transsaccadic feature integration in a different manner, to constrain the possible underlying processes. We expect that, if transsaccadic integration is a process that occurs later in the visual processing stream, transsaccadic integration is saccade landing point invariant, as earlier visual processing areas show a smaller receptive field size, on average (Smith, Singh, Williams, & Greenlee, 2001).

Research into transsaccadic feature integration has shown that the temporal and spatial characteristics of a stimulus may affect how human observers weigh both pre- and postsaccadic visual input. For instance, we are generally predisposed to overweighing the foveal input (Ganmor et al., 2015; Wolf & Schütz, 2015). This is not entirely unsurprising, as postsaccadic visual input is generally foveated and sampled with higher acuity than presaccadic visual input. Furthermore, research has shown that the distance between the fovea and an object of interest affects how visual feature representations are weighed pre- and postsaccadically (Oostwoud Wijdenes et al., 2015). In the study by Oostwoud-Wijdenes et al. (2015) observers were instructed to report the color of one of three objects, after making a saccade. Observers saw the objects before and after the saccade. Unbeknownst to the observers, the objects changed color during the saccade. Observers reported a mixture color (i.e., integrated pre- and postsaccadic color) for all the objects. Crucially, one of the objects was positioned close to the presaccadic point of fixation, another was positioned close to the postsaccadic point of fixation, and the third object was positioned at an intermediate location. The authors found that observers reported a mixture color that was weighed more towards the presaccadic color (before the color change) when the object that had to be reported

was the one closest to the presaccadic point of fixation. Additionally, when reporting the color of the object that was closer to the postsaccadic point of fixation, observers responded with a mixture color that was weighed more towards the postsaccadic color. Lastly, an intermediate mixture color was reported for the objects at the intermediate location. From this experiment, as well as further experiments by Oostwoud-Wijdenes et al. (2015) where visual information was manipulated by adding presaccadic or postsaccadic noise, the authors concluded that the weights of pre- and postsaccadic information during transsaccadic feature integration is affected by the reliability of visual input. Furthermore, they show that the reliability of visual input is directly affected by point of fixation.

The observation that distance of visual input relative to the fovea affects the reliability of our estimates of that input and in turn how we integrate information is interesting, given that saccades show relatively large variance in their landing point. If the distance between the landing point of the eye and the target is the only determining factor, it would lead to different weights between pre- and postsaccadic input with every saccade. Especially when using color stimuli, as research has shown that cone (color receptor) density is highest in the central 0.032 deg^2 of the surface area of the fovea (Curcio, Sloan, Kalina, & Hendrickson, 1990). Cone density drops off steeply with increasing distance to the fovea, with a factor of 10 with each $\sim 3.5^\circ$ increase in distance from the fovea (Curcio et al., 1990). Alternatively, transsaccadic feature integration could be robust against within-subject variance in motor execution as visual attention (where visual information is sampled) and point of fixation (the center of gaze) may be dissociated across saccades. Typically, attention shifts towards the location of the intended saccade target, rather than towards the saccade landing point (Deubel, 1995; Deubel & Schneider, 1996; Klapetek, Jonikaitis, & Deubel, 2016; Szinte, Jonikaitis, Rolfs, Cavanagh, & Deubel, 2016; Van der Stigchel & de Vries, 2015). In a study by Van der Stigchel and De Vries (2015), observers performed an oriented bar discrimination task at the location of their saccade target (an annulus) or at a neighboring location. The bar was presented within an annulus with different timings with respect to saccade onset. In certain trials, a salient distractor was presented, resulting in saccades that landed in between the saccade target and salient distractor due to saccade averaging (i.e., a global effect). During the distractor present trials, observers were not able to discriminate the target in between the saccade target and the distractor more accurately, even though saccades landed in between these positions. Instead, observers remained best at identifying the orientation of the bar at the intended saccade target, regardless of where the saccade landed. The authors concluded that saccades

and attentional processes linked to saccade execution can target different spatial locations. This spatial dissociation effect has been expanded by Wollenberg, Deubel, and Szinte (2017), who showed that presaccadic attention was equally distributed to both saccade targets. Effectively, this study rules out mandatory coupling of attention to the saccade landing point.

In the current study, we will examine whether and how saccade landing point affects transsaccadic integration of visual features. In the experiments, observers were tasked with reporting the color of a saccade target, which was presented shortly before and after the saccade, similar to the study of Oostwoud-Wijdenes et al. (2015). In our analysis, we contrasted color reports for trials in which saccades landed close to the colored target with color reports for trials in which saccades landed further away from the colored target. We expected that, if deployment of attention can indeed be separated from saccade landing point and the focus of attention is crucial for transsaccadic integration, then pre- and postsaccadic information is weighed and integrated in the same way regardless of whether saccades land further from the intended saccade landing point. However, since we use color stimuli, and color perception is less accurate further away from the fovea, it is also plausible that pre- and postsaccadic visual input is weighed based on saccade landing position. Crucially, we opted to use Bayesian statistics. Whereas traditional/frequentist statistics, which can only reject or lack the evidence to reject the null, Bayesian hypothesis tests can differentiate evidence for the null, evidence for the alternative hypothesis, or inconclusive evidence (Wagenmakers, Lodewyckx, Kuriyal, & Grasman, 2010). We used two measures of transsaccadic integration to investigate this hypothesis in two experiments: reduction of error and changes in bias in reporting the color of the saccade target.

Experiment 1: Effect of saccade landing point on color reports

Methods

Observers

Observers ($N = 16$; nine male, seven female; mean age = 20.8) reported normal or corrected-to-normal vision. The experiment took 90 min to complete. Observers signed an informed consent form prior to the start of the experiments. The observers were compensated for their time with €6 an hour. Both experiments were conducted in accordance with the declaration of Helsinki of 1964, and were approved by the Faculty Ethics committee (FETC) of Utrecht University.

Apparatus

The experiment was conducted in a darkened lab. Observers supported their head with a chin rest at 70 cm distance from an Asus ROG Swift PG278Q monitor (60.1×34.0 cm, $2,560 \times 1,440$ pixels, 100 Hz; pixel response time 1 ms; AsusTek Computer Inc., Taipei, Taiwan). To make sure that color mixing did not occur due to persistence of the pixels of the screen, the Ultra-Low Motion Blur setting was turned on, and set to a pulse width of 50. The gamma value was adjusted to linearize luminance within RGB channels prior to the experiment.

To investigate the timing of visual presentation we used a photodiode (placed in the bottom-left corner of the screen), connected to the printer port of the EyeLink host-pc, which output the measured luminance in the EyeLink data file. We chose the two hues in the color space used in the experiment (described below) with the largest luminance discrepancy (34° and 64° hue values). We set the threshold for detection at 80% luminance (of the difference in luminance between the two hues), and dark detection at 20% luminance. We presented 1,000 repetitions of 10 frames of the hue at 34° , followed by 10 frames of the hue at 64° . We recorded the luminance of a screen-sized rectangle. Screen settings matched the screen settings in the experiment. The delay between the draw call and response on the screen was around 11 ms ($M = 10.8$, $SD = 5.5$, $Mdn = 10$, $IQR = 9\text{--}10$). There may be a small portion of trials in which the pixels had not reached the desired values within one frame. In these measurements we found that the desired luminance was only reached after 20 ms. If this proportion holds for our experiment, it would affect 6% of the trials (as shown in Supplementary Figure S1).

Next, we alternated between 64° in hue in our color space and black. When we set the threshold for brightness detection at 80% luminance, we see that the luminance is only reached after 20 ms ($M = 20.5$, $SD = 3.2$, $Mdn = 20$, $IQR = 20\text{--}11$, Supplementary Figure S1). This indicates that the screen may take an additional frame to update when going from black to one of our colors used in the experiment. It does seem to be an additional frame, as the “missing” frame is followed by nine subsequent frames. From this we conclude that when changing the color, the new color is usually reached within a single frame, whereas in conditions where we transition from color to black, there may be one frame in which the pixels have not reached the desired luminance (a ~ 20 ms delay between the draw call and presentation). Therefore, it seems stimulus presentation was largely as intended and that the screen used is appropriate for stimulus presentation in the experiments.

The left eye was recorded at 1,000 Hz with an EyeLink 1000 (SR Research Ltd., Canada), calibrated with the native 9-point calibration procedure. Eye-

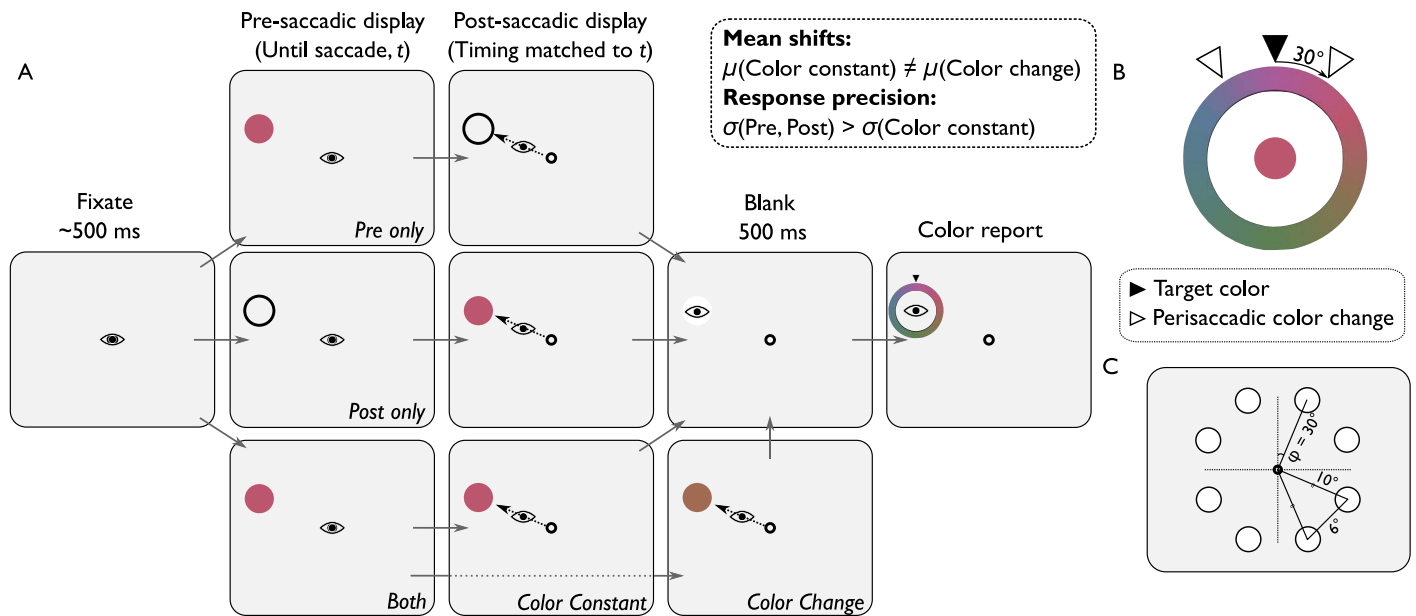


Figure 1. The procedure of Experiment 1. (A) The timeline of the different conditions in Experiment 1. Note that the experiment was presented in inverted contrast (background was black; annulus was white). (B) The color wheel used in all experiments, the distance between the white and the black arrows indicate the magnitude of the color change in the experiment. (C) Stimuli were presented at one of eight locations relative to the fixation point, as indicated by the circles.

movement events were detected offline using the native EyeLink saccade and fixation detection algorithms. The experiment was programmed in Python 2.7.3, using the *Pygaze* library for eyetracking research (Dalmaijer, Mathôt, & Van der Stigchel, 2014). Colors were generated using the HSL_{uv} Python library (Boronine & McGinley, 2017). The data was analyzed in R, using the *BayesFactor* package (Morey & Rouder, 2015; R Development Core Team, 2008).

Stimuli

Stimuli were presented on a black background (1.1 cd/m^2). Observers fixated the center of the screen, indicated by a small annulus of 0.5° (4.2 cd/m^2). The saccade target was a colored circle (radius = 0.5° , luminance = 9.8 cd/m^2), which could appear at one of eight locations. The targets appeared at an eccentricity of 10° and at an angle of 30° or 60° with respect to the cardinal axes (see Figure 1C). The color space used in the experiment was HSL_{uv} , a perceptually uniform color space expressed in Hue, Saturation, and Lightness parameters. Saturation and lightness were kept at a value of 50 and hue was randomly selected from a uniform distribution ranging from 0° to 360° . Observers were instructed to report the color of the target on a color wheel. The polar angle of the response on the color wheel corresponded with the angle in hue of the color space. In the Color change condition the hue of the saccade target shifted by $\pm 30^\circ$ (see Figure 1B).

Lastly, the target could be replaced with a white annulus (with a radius of 0.5° with a border of 0.2° , $\text{cd/m}^2 = 10.4$) either before (Post Only; the condition name refers to when the color was visible) or after a saccade (Pre Only). After the postsaccadic stimulus information was presented, the target was removed from the screen to reduce the influence of corrective saccades.

Procedure

Each observer ($N = 16$) completed 448 trials evenly distributed across all conditions. Trials were counter-balanced across the experimental conditions (Pre Only, Post Only, Color Constant, and Color Change), as well as the target location (one out of eight locations), resulting in 14 trials per observer per condition. For the analyses, target location was collapsed (thus resulting in a maximum of 112 trials per observer per condition). Observers were instructed to make a saccade to the target and to report the color of the saccade target. There were four experimental conditions, which relate to when the color of the target was visible, and whether the color changed (see Figure 1A). The stimulus either turned into an annulus after a saccade was made (Pre Only; 25% of trials), started as a white annulus and became colored after a saccade was made (Post Only; 25% of trials) or was colored before and after the saccade (Both; 50% of trials). Trials in the Both condition were divided into Color Constant (25% of total trials) and Color Change trials (25% of total

trials). In the Color Change trials, the hue of the target shifted by $+30^\circ$ or -30° . As a measure of feature integration we (a) investigated whether responses in the Color Change trials were a mixture of presaccadic and postsaccadic hue, when compared to the Color Constant trials, and (b) investigated whether observers were more precise in reporting the color in the Color Constant (both Pre- and Postsaccadic color) trials as compared to the Pre Only and Post Only trials.

A typical trial occurred as follows: Observers fixated a fixation point in the center of the screen until a saccade target appeared (a circular object). Observers were instructed to execute a saccade as quickly as possible to the saccade target. The (online determined) saccadic reaction time was calculated as the difference between saccade target onset and the recorded gaze position leaving a 1.5° area of interest around fixation. We matched the duration that the stimulus remained on screen postsaccadically to the saccadic reaction time (SRT; i.e., the amount of time the stimulus was visible presaccadically). Then, all stimuli were removed from the screen for 500 ms. Finally, observers reported the color of the saccade target by clicking on a color wheel. The selected color was shown in a small circle at the center of the color wheel; observers confirmed their answer by pressing the space bar. Observers were aware that the saccade target was either colored before the eye movement, after the eye movement, or both. Unbeknownst to the observer, we included trials in which the color of the saccade target changed during the saccade (a hue change of $\pm 30^\circ$). No observers reported being aware of the color change.

Observers first completed twenty practice trials to familiarize themselves with the task, where conditions were randomly assigned. Observers were encouraged to make fast saccades (SRT shorter than 250 ms), and received feedback on their saccade latency after each trial in the practice block through an onscreen message. Furthermore, participants were instructed to not make any additional saccades after directing their gaze toward the target. If, during the practice block, mean SRT was higher than 250 ms, another twenty practice trials were completed. Observers completed 448 trials in 14 blocks, with short breaks between the blocks, and were debriefed at the end of the experiment. At the end of each block, observers received feedback on their mean SRT, and were encouraged to execute saccades faster if their latency was higher than 250 ms. Debriefing consisted of a digitized questionnaire where observers were asked whether they had perceived the color change. None of the observers reported seeing the color change in either the questionnaire or when questioned at the end of the experiment by the experiment leader.

Data preprocessing

Data preprocessing consisted of two main steps. First, we recalculated the saccade latency and amplitude using offline saccade detection. Then we recoded the target and distractor locations to one quadrant. Saccades were detected offline with the default Eyelink saccade detection algorithm. For all analyses on saccade metrics, we chose the first saccade after the target had been presented, but only if the saccade was started before the postsaccadic probe presentation.

To be able to compare saccade landing distance, we recoded all target locations to the same location. We converted the Euclidian coordinates of targets, and saccade landing points to polar coordinates. In polar coordinates, ϕ is the counterclockwise angle from the horizontal meridian (in degrees) and ρ is the saccade amplitude (in degrees visual angle). Then, we recoded the target locations by collapsing all the target quadrants into one quadrant (see Figure 1C). This was accomplished by calculating $\phi = \phi - 0^\circ$ from trials in quadrant 1, $\phi = \phi - 90^\circ$ in quadrant 2, $\phi = \phi - 180^\circ$ in quadrant 3, and $\phi = \phi - 270^\circ$ quadrant 4. By subtracting a set amount of degrees from ϕ based on the quadrant, we ended up with all targets represented in one quadrant.

Next, once all targets were recoded to the same quadrant, we recoded the location once more so that the target stimulus was always presented at $\rho = 10^\circ$ and $\phi = 30^\circ$ from the vertical meridian. We did so by calculating $\phi = 90^\circ - \phi$ in trials where the target was presented at 60° degrees. After this final preprocessing step, each trial was recoded in the same way so that the saccade landing points were represented in the same way (e.g., a saccade with a vector of $\rho = 10^\circ$, $\phi = 30^\circ$ landed exactly on target).

Lastly, we recoded the dependent variable for our analyses. For all our main analyses we entered the difference between the given answer and the presaccadic color as the dependent variable. Where 0° indicates the presaccadic color on the color wheel, positive values indicate answers with clockwise deviations from 0° and negative values counterclockwise deviations from 0° in the color wheel. In the Color Change trials the postsaccadic color was either 30° (clockwise) or -30° (counterclockwise) from the presaccadic color. For the counterclockwise color change trials, we recoded the direction of the color space by multiplying the reported color by -1 , so that for every trial the postsaccadic color was at 30° (clockwise) from the presaccadic color.

Data exclusion

From the 7,407 trials where a saccade was recorded we excluded 285 trials where a gaze sample was recorded further than 2° from fixation before the target was presented. We excluded 63 trials where a saccade

landing point was detected in the wrong quadrant. Furthermore, 198 trials were excluded where the saccade amplitude was lower than 6° or higher than 14°, and 73 trials where the saccade latency was higher than 250 ms. Lastly, we excluded 161 trials in which a corrective saccade was detected, as defined by a saccade that was initiated after the first saccade, which landed before the stimulus was removed from the screen. Some trials did not meet several of these criteria. After exclusion, one participant had less than 50% of the trials left (119 out of 448 trials); this participant was excluded from further analysis. After excluding the participant, 6,493 trials were left across all participants. The average amount of trials left per observer was 404 trials ($SD = 44$, range 256 to 434 trials).

Statistical analyses

Because of the nature of the design, the hypotheses suggesting that saccade landing point does and does not influence transsaccadic integration are equally valid. Therefore, we opted for Bayesian statistics. Bayesian statistics allow us to differentiate between two hypotheses, rather than only rejecting one hypothesis, as in frequentist testing (for an overview of Bayesian Hypothesis Testing, see Wagenmakers et al., 2010). The outcome of a Bayesian analysis is a Bayes Factor (BF) which is the ratio of evidence for one hypothesis over another. For example, a test which shows $BF = 100$ for one model indicates that this model is 100 times more likely than the model it is tested against. To interpret the strength of evidence of a BF, Kass and Raftery (2012) have provided guidelines. A BF of between 1 and 3 is described as providing evidence that is “not worth more than a bare mention.” A BF of 3 to 20 provides “positive” evidence, 20 to 100 “strong” evidence, and above 100 “very strong” evidence (Kass & Raftery, 2012). In the manuscript, we report all BFs in favor of one model over the other, where BF_{10} is the evidence for the alternative hypothesis over the null hypothesis and BF_{01} is the evidence for the null hypothesis over the alternative hypothesis (since BF_{10} is equal to BF_{01}^{-1}). In our design, BF_{10} indicates evidence for the alternative hypothesis (gaze position affecting color reports), whereas BF_{01} is evidence for the gaze position invariance hypothesis. First, we divided the data into two halves using a median split on saccade landing distance. Then, using Bayesian modeling averaging, we investigated whether observers reported a different color between saccades that landed closer (lower or equal to the median) or further from the target (higher than the median). The model included three fixed effects: a fixed effect for Condition (Pre Only, Post Only, Color Constant, or Color Change), and a fixed effect for Landing Distance (close vs. far), and an interaction effect between Condition and

Landing Distance. Furthermore, a random intercept was added per observer. We compared models that included the fixed effects to models that did not, as evidence for inclusion of the parameter (Bayesian Model Averaging; Hoeting, Maigan, Raftery, & Volinski, 1999; consistent with the implementation in JASP, see Wagenmakers, 2015). All reported statistics are within-subject statistics. All priors for Bayesian tests were set to a Cauchy distribution centered at 0° (or 30°) with a width of 0.707° (Morey & Rouder, 2015; Wagenmakers et al., 2010).

To investigate whether observers integrated information across saccades, we used Bayesian t tests. Our criterion for integration in Experiment 1 was, in the Color Constant condition, a response similar to 0°. For the Color change condition we tested for a response in between 0° (presaccadic color) and 30° (postsaccadic color). With a Bayesian t test, we examined whether we collected sufficient evidence for either the hypothesis that the difference between two (scaled) conditions is more likely to be zero (BF_{01} : $\delta = 0$), or different from zero (BF_{10} : $\delta \neq 0$). Similarly, we used Bayesian t tests to compare the standard deviation of the responses in the Pre Only and Post Only condition to the standard deviation of the responses in the Color Constant condition. For Bayesian tests, we report the Bayes Factor (BF_{10} or BF_{01}) and the 95% credible intervals (95% CI).

Additionally, we used an optimal observer model as described by Ganmor et al. (2015). We calculated the bias in the Color Change condition ($\hat{\mu}_{ColorChange}^*$) and estimated the standard deviation in the Color Constant condition ($\hat{\sigma}_{ColorConstant}^*$). First, we calculated the weighted sum of observer estimates using the following formula $\hat{\theta}_{ColorConstant}^* = w_{post}^* \hat{\theta}_{post} + w_{pre}^* \hat{\theta}_{pre}$, where

$$w_{post}^* = \frac{\sigma_{post}^{-2}}{\sigma_{post}^{-2} + \sigma_{pre}^{-2}}, \text{ and } w_{pre}^* = 1 - w_{post}^*. \text{ Next, we calcu-}$$

lated the expected response (according to the optimal observer model) in the Color Change condition given the calculated weights for each observer, where $\hat{\mu}_{ColorChange}^* = w_{post}^* (\theta \times \mu_{post}) + w_{pre}^* (\theta \times \mu_{pre})$. We also calculated the optimal standard deviation with $\hat{\sigma}_{ColorConstant}^* = \left(\sigma_{post}^{-2} + \sigma_{pre}^{-2} \right)^{-2}$. We compared the calculated estimates to the observed means in the color change condition using a paired Bayesian t test. Lastly, as noted by Ganmor et al. (2015), the maximal reduction of variance, given the model, would occur when the standard deviation of the Post only and Pre only condition are equal to each other. However, since we matched the time of the presaccadic presentation to the postsaccadic presentation, and foveal processing is of higher resolution, we expect that $\sigma_{post} < \sigma_{pre}$, thus resulting in a higher weight of postsaccadic information and a smaller reduction in variance due to optimal integration. In addition, we expect that $\sigma_{both} < \sigma_{post}$, but

that this difference will be minimal, as the largest reduction in error is expected when the reliability of presaccadic and postsaccadic visual input is roughly similar ($\sigma_{post} = \sigma_{pre}$, which can be accomplished by for example, lowering the contrast of the target during the saccade; Ganmor et al., 2015; Wolf & Schütz, 2015). In our design the stimuli were of equal strength before and after the saccade.

Results

To investigate the effect of saccade landing point on transsaccadic perception, we compared color reports across saccades that landed close to the target and color reports after saccades that landed far from the target. There were four conditions in our experiment, relating to when the color of the target was visible (Pre Only, Post Only, Color Constant, and Color Change). We observed that observers reported the color of the saccade target in the Pre Only condition, that is, we found evidence that the difference between the color of the saccade target and response was 0, $BF_{01} = 7.08$, 95% CI $[-3.39^\circ$ to $0.17^\circ]$. Similarly, observers reported the target color in the Post Only condition, $BF_{01} = 34.7$, 95% CI $[-0.87^\circ$ to $0.70^\circ]$, and the Color Constant condition, $BF_{01} = 22.49$, 95% CI $[-1.12^\circ$ to $0.38^\circ]$.

We validated the timing of the color transitions revealing that the screen update happens around 20 ms after saccade onset (median = 20 ms, IQR = 17–24 ms, shown in Supplementary Figure S2). Here, the draw call is corrected to account for the extra 10 ms it takes for the screen to update. The screen update happens around 20 ms before the saccade ends ($Mdn = -23$ ms, IQR = -30 to -17 ms). In trials in which the stimulus is transitioning into black, another 10 ms should be added to these numbers.

Color reports

We expected that observers in the Color Change condition reported a color that is a mixture (in between) of the presaccadic and the postsaccadic color. In these trials, a response of 0° would indicate the presaccadic color whereas a reported hue of 30° would indicate the postsaccadic color was reported. We observed that observers indeed neither reported the presaccadic, $BF_{10} = 1.15 \times 10^{468}$, nor the postsaccadic color, $BF_{10} = 4.91 \times 10^9$ but a color in between, 95% CI $[26.27^\circ$ to $27.86^\circ]$. Second, we compared the standard deviation of the responses in the Pre Only and Post Only condition to the Color Constant condition. The standard deviation was higher in the Pre Only condition (average $SD = 36.5^\circ$) than in (a) the Post Only condition, average $SD = 15.9^\circ$, $BF_{10} = 12,638$, 95% CI $[13.36^\circ$ to $24.73^\circ]$, (b), and the Color Constant

condition, average $SD = 15.5^\circ$, $BF_{10} = 57254$, 95% CI $[14.53^\circ$ to $24.60^\circ]$. We found evidence for no difference between the Post Only condition and the Color Constant condition, $BF_{01} = 2.83$, 95% CI $[-0.57^\circ$ to $1.28^\circ]$. Thus, observers integrated pre-and postsaccadic information in terms of mean shifts, but this did not reduce the absolute error. All participants had a smaller standard deviation in their responses in the Post Only condition (mean difference = 19.8° , minimum = 7.01, maximum = 36.62). These results seem consistent with prior research using nondegraded, postsaccadic stimuli (Oostwoud Wijdenes et al., 2015).

Effect of landing distance on color reports

Next, we investigated the effect of saccade landing distance on reported color. We divided landing distance into two distances (close, far) using a median split (median distance = 1.18° , IQR = 0.75° – 1.80°). The saccade landing points are shown in Figure 2A. For each condition (Pre/Post Only, Color Constant/Change) we calculated the mean response and standard deviation of the responses per observer, per landing distance. We constructed a Bayesian linear mixed model with mean reported color as dependent variable, and fixed effects for Condition, and Landing distance (median split), as well as an interaction between Condition and Landing distance. The results of the analysis are shown in Figure 2B, and the Bayesian Modeling Averaging statistics are shown in Table 1. The analysis reveals a main effect of Condition, $BF_{10} = 5.10 \times 10^{61}$, no main effect for Landing distance on reported color, $BF_{01} = 2.06$, and evidence against an interaction between Landing distance and Condition, $BF_{01} = 45.87$. Similarly, for the standard deviation of the responses (Figure 2C) we observed a main effect for Condition, $BF_{10} = 3.84 \times 10^{32}$, no evidence for a main effect for Landing distance, $BF_{01} = 2.35$, and evidence against an interaction effect, $BF_{01} = 310.84$. When saccades landed further away from the saccade target, and postsaccadic visual input is presumably sampled at a lower resolution, yet the reported color remains the same.

Optimal observer model

Next, we investigated color reports across saccades in an optimal observer model. Such models provide insights into how observers could theoretically combine both presaccadic and postsaccadic information in a way that utilizes both sources of information in a way that combines the information in a statistically optimal manner. We calculated the weights that observers attributed to pre-and postsaccadic information based on the variance of the color reports in the Pre Only and Post Only condition. These weights were used to

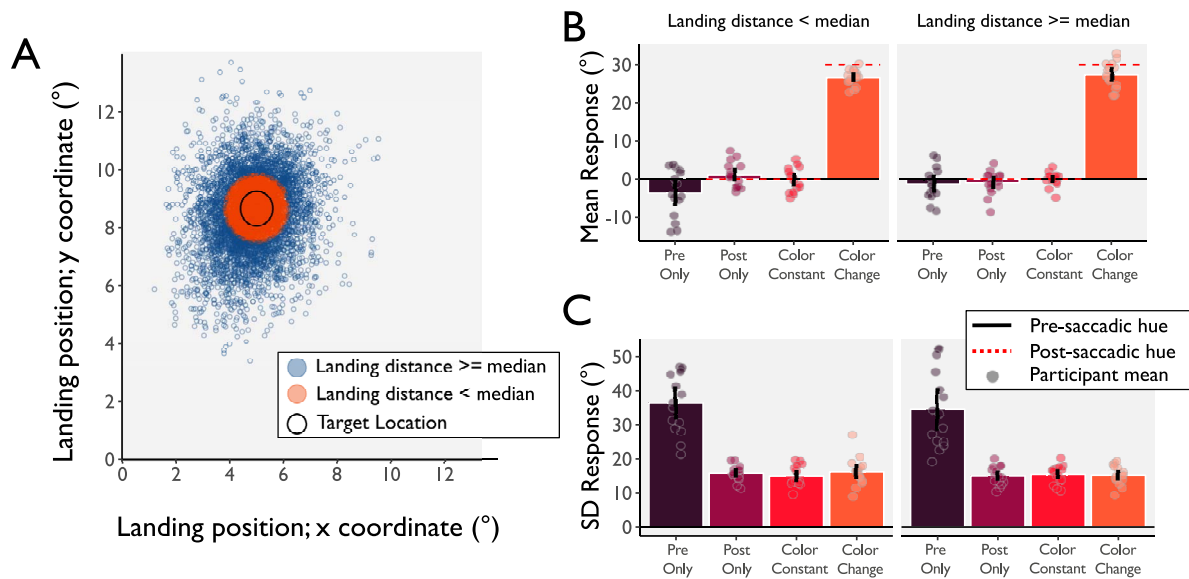


Figure 2. Main results Experiment 1. (A) Observers made saccades to a target (here the black circle). Each dot represents the landing point of one saccade. The two colors represent the median split, close versus far saccades. (B) and (C) Average responded color per condition and standard deviation of responses per condition, respectively. The bars show the grand mean, the black dots the observer means, and the error bars the 95% CI. The horizontal black lines indicate the presaccadic color in each condition (if present) and the horizontal red dashed lines indicate the postsaccadic color in each condition.

calculate the optimal combination of pre and post information in the Color Constant and Color Change condition and compared this to the observed standard deviation in the Color Constant condition and the observed mixture colors in the Color Change condition. We investigated two measures within the optimal observer model: (a) bias, which is reflected in the mean reported color in the Color Change and Color Constant condition, and (b) precision, which is reflected by the response error variability. Note that in prior analyses we only observed shifts in the mean (differences in bias), and did not find a reduction in variability. The analysis will provide insight into whether observers could (theoretically) combine pre-saccadic and postsaccadic information in a more efficient manner. Lastly, we investigated the effect of

saccade landing point (close vs. far) on presaccadic and postsaccadic weights.

The estimated values, as compared to the observed (mean) values are shown in Figure 3. The observed standard deviation in the Color Constant condition was 15.1° ($SD = 2.52$). The optimal standard deviation for the Color Constant condition, based on the responses given in the Pre Only and Post Only condition was 13.94° ($SD = 1.86$), which indicates that it was possible for participants to improve further (respond more precisely). The observed standard deviation in the Color Constant condition was higher than the optimal standard deviation, $BF_{10} = 4.55$, 95% CI $[-1.85$ to $-0.16]$. The grand mean observed bias was 27.11° ($SD = 2.22$), whereas the estimated bias in the optimal observer model was 24.51° ($SD = 2.59$). We found that the observed bias was more weighed

Model parameters	Mean error		SD of error	
	BF_{10}	Error	BF_{10}	Error
Condition + observer	3.06×10^{61}	0.79%	8.70×10^{32}	1.16%
Landing distance + observer	1.96×10^{-1}	2.63%	5.65×10^{-1}	0.93%
Condition + landing distance + observer	6.22×10^{60}	2.61%	6.42×10^{31}	0.91%
Condition * landing distance + observer	3.55×10^{60}	15.2%	3.92×10^{30}	9.32%
Observer	1.00	<0.01%	1.00	<0.01%

Table 1. Parameter estimates for Bayesian Model Averaging analysis investigating how saccade landing distance (median split) affects mean error and standard deviation of errors. Notes: The * symbol denotes a model with both main effects and interaction effects between the parameters. Bayes Factors have been rescaled to the random effects model (Observer only) for readability.

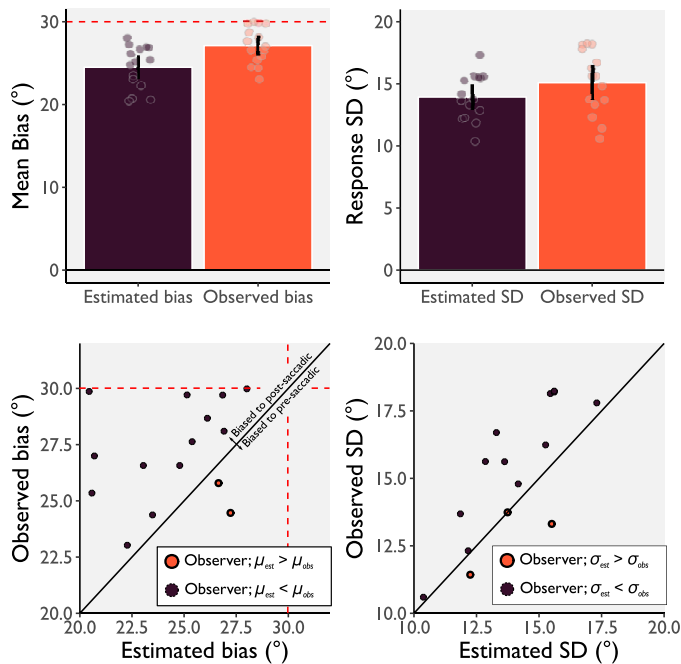


Figure 3. Results from optimal observer model analysis in Experiment 1. (A) The purple bars indicate the estimated bias according to the optimal observer model, whereas the beige bars indicate the observed bias, that is, the response in the Color Change condition. The right figure shows the estimate standard deviation versus the observed standard deviation, that is, the standard deviation in the Color Constant condition. The bias (left plot) indicates that observers are biased towards postsaccadic visual information, whereas the standard deviation (right plot) indicates that participants do not reach optimal performance. The dots indicate observer means, the bars indicate 95% CI. (B) Observer averages for both the bias and standard deviation. The reference line indicates an optimal trade-off between pre- and postsaccadic visual input. Most observers overweigh the postsaccadic (foveal) input. The red dashed line in both left-hand graphs indicates the postsaccadic color of the target.

towards to postsaccadic visual input (the observed response is closer to 30° than the optimal response), $BF_{10} = 12.29$, 95% CI [−3.90 to −0.76]. In line with prior studies, observers are integrating presaccadic and postsaccadic information close to optimality.

Lastly, we investigated the effect of saccade landing distance on bias and precision. In particular, we were interested to see whether observers weighed presaccadic and postsaccadic information differently if saccades landed further from the saccade target. Using a paired Bayesian t test, we compared the estimated weights for saccades that landed close and saccades that landed further away. The average weight of presaccadic input, w_{pre} (where the postsaccadic weight is given by $w_{post} = 1 - w_{pre}$), for saccades that land nearby was 0.176, IQR = 0.069–0.336. The average w_{pre} for saccades that landed further away from the saccade target was 0.187, IQR =

0.062–0.332. There was no difference in estimated weights for saccades that landed closer or further away, $BF_{01} = 3.36$, 95% CI [−0.03 to 0.02]. Consistent with our prior findings, the color reports did not change as the saccade landing point deviated more from the saccade target.

Experiment 2: Color reports across saccades with larger landing point deviations

In the previous experiment, we found no effect of saccade landing point on reported hue. The saccade landing point variability in Experiment 1 was relatively small, however. To test our hypothesis in a more extreme situation, we set out to investigate trans-saccadic color reports, under deviations that exceed the ones found in everyday situations (e.g., regular oculomotor error such as in Experiment 1). We removed the Pre Only and Post Only conditions from the experiment, as we found no effect of reduction of error when compared to the Color Constant condition. We replaced these conditions with Distractor Present trials. In these trials a salient distractor is presented at the same time as the saccade target. Prior research has shown that by presenting a salient object near a saccade target, cause saccades to land at the geometric mean of these objects (Coren & Hoenig, 1972; Cronin & Brockmole, 2016; Van der Stigchel & Nijboer, 2011). We placed the distractor object at 6° from the target. Based on the observation that global effect saccades land (on average) on the geometric mean between the target and distractor, we expect an average deviation of the saccade of 3°. Through this method, saccade landing points will deviate further from the saccade target than in Experiment 1 (where the median deviation of saccade landing point was 1.18°).

Methods

Observers, stimuli, and procedure

Given that we debriefed observers at the end of Experiment 1, none of the observers that participated in Experiment 1 participated in Experiment 2 ($N = 16$; six male, 10 female; mean age = 22.3). In Experiment 2, a white distractor object could be presented simultaneously with the saccade target (Figure 4, radius = 0.5°, 31.2 cd/m²). The saccade target and the distractor were presented at an eccentricity of 10° visual angle from fixation (Figure 1C). The distractor was always presented within the same quadrant as the saccade target, at a distance of 6° visual angle from the target. The size of the stimuli and distance between distractor

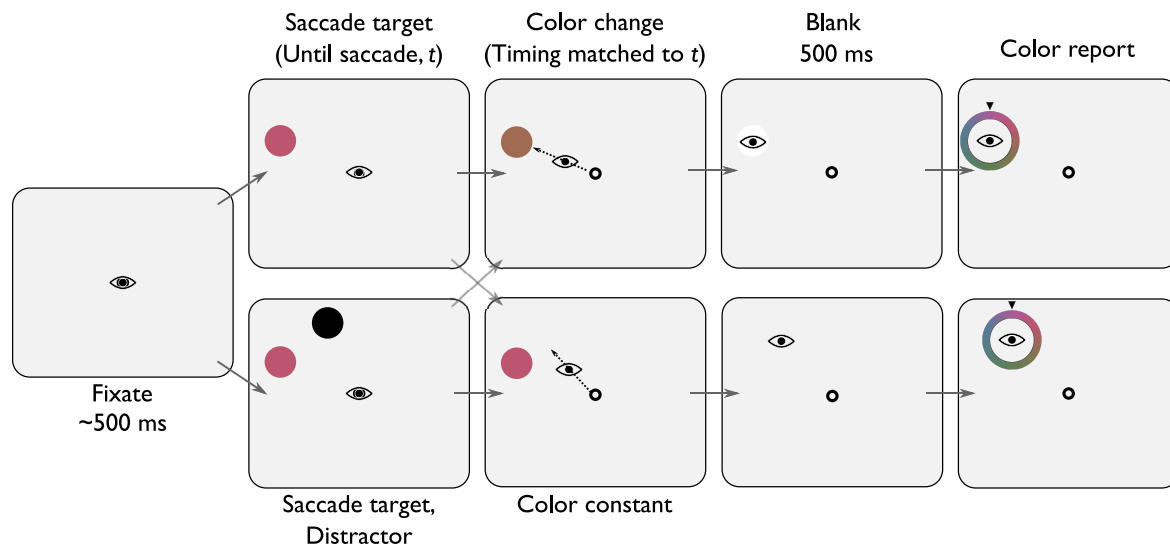


Figure 4. Procedure of Experiment 2. In this experiment, a salient distractor object could appear at the same time as the saccade target (colored circle). Note that the figure is presented in inverted contrast, in the experiment the background was black and the distractor was white. Furthermore, the color change as shown here is exaggerated for illustrative purposes.

and saccade target were chosen to favor a strong global effect, based on prior research (Van der Stigchel, Heeman, & Nijboer, 2012).

Data preprocessing and exclusion

The number of recorded trials was identical to Experiment 1. Observers completed 448 trials, counterbalanced across the experimental conditions (Color Constant/Change and Distractor Absent/Present). Thus, a maximum of 112 trials was recorded per observer per condition after collapsing across target locations (eight possible locations). We excluded trials (from a total of 6,990 trials in which a saccade was detected) based on the same criteria as in Experiment 1. First, we excluded a trial if a gaze sample was recorded further than 2° from the fixation point before the target was presented (0 trials). Second, a trial was excluded if a saccade landing point was detected in a quadrant where no target was present (10 trials). Third, if a saccade had an amplitude lower than 6° or higher than 14° (606 trials). Fourth, if a saccade had a latency of higher than 250 ms (32 trials), and lastly, if a corrective saccade was made (180 trials). After exclusion, one participant had less than 50% of trials left; this participant was excluded (159 trials left of 448). Thus, after exclusion, 5,989 trials were left for analysis (mean trials per observer = 399, $SD = 38$, range 310 to 440 trials).

Statistical analyses

The analyses of Experiment 2 were largely similar to the analyses in Experiment 1. All reported statistics

are within-subject statistics. First, we examined whether our saccade landing point manipulation (presenting a distractor) was successful in increasing saccade landing point deviations (i.e., whether there was a global effect). We compared the Euclidian saccade landing distance from the target in the Distractor Absent trials to the Distractor Present trials. To quantify this, we chose to use a Bayesian t test. To quantify the difference in color reports between Distractor Present and Distractor Absent trials we ran a full factorial linear mixed model that predicted the difference between the reported hue and the presaccadic hue. The model included three fixed effects: a fixed effect for Color (change vs. constant), a fixed effect for Distractor Presence (present vs. absent), and an interaction effect between Color and Distractor Presence. Furthermore, a random intercept was added per observer. The rest of the statistics largely follow the procedure of Experiment 1.

Results

We investigated the effect of saccade landing point on color reports when saccades deviate far from the saccade target by making use of the global effect. We manipulated the landing points of saccades by showing a salient distractor in half of the trials (Distractor Present/Absent) at the same time as a colored saccade target. Observers were tasked with indicating the color of the saccade target on a color wheel. In half of the trials the color of the saccade target changed during the saccade (Color Change/Constant).

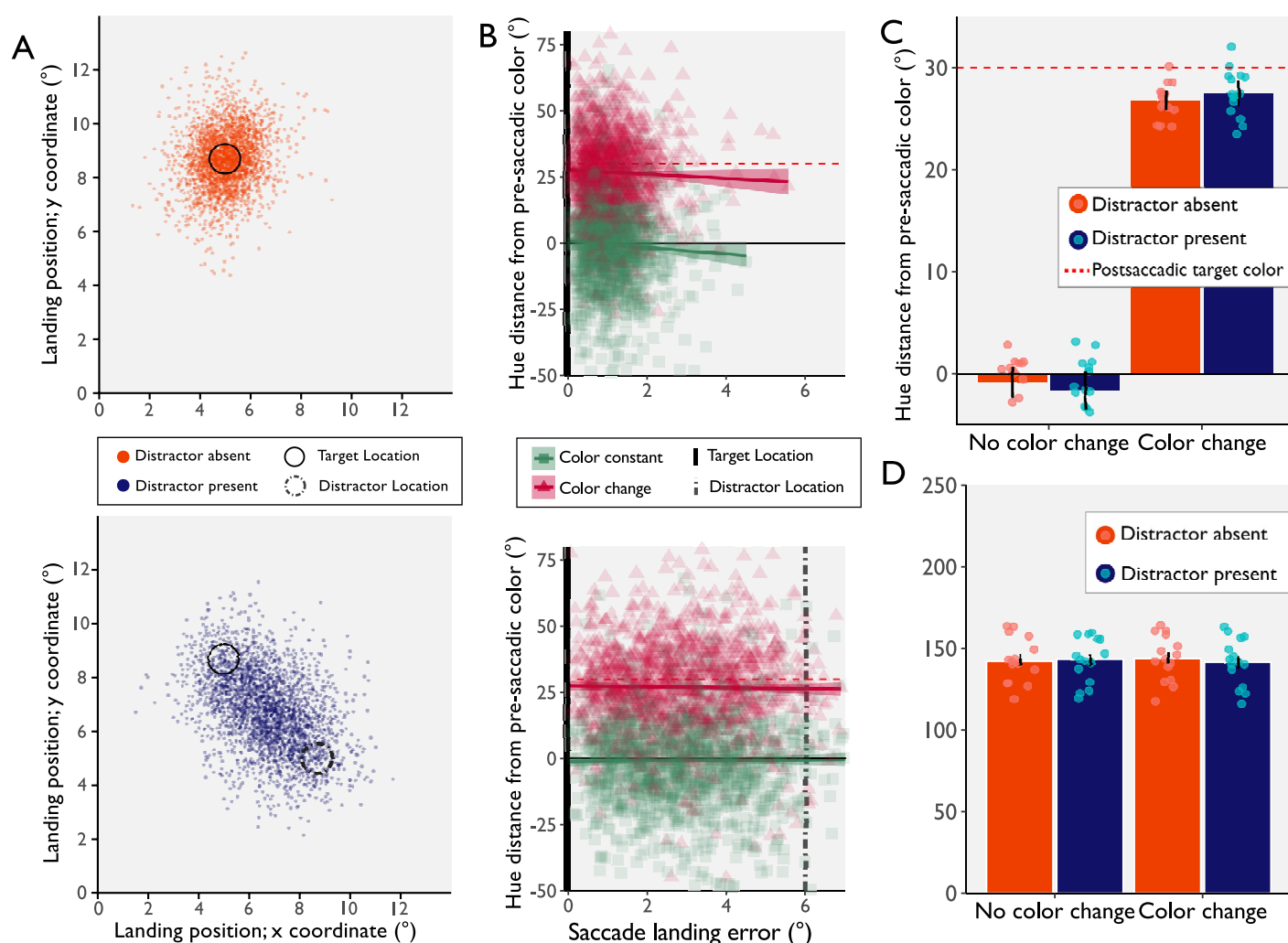


Figure 5. Results from Experiment 2. (A) Saccade landing points in the Distractor Absent (upper panel)/Present (lower panel) conditions. On average, saccades landed farther away from the saccade target in the Distractor Present condition than in the Distractor Absent condition. (B) Linear fit to saccade landing error and reported color in the Distractor Absent (upper panel)/Present (lower panel) conditions. None of the slopes were different from 0, indicating no effect of saccade landing distance. Shaded regions indicate the standard error of the fit; the transparent points are individual responses. (C) Average reported color per condition, as indicated by the colored bars. No difference was observed between Distractor Absent and Distractor Present conditions. (D) Median saccade latency across conditions, as indicated by the colored bars. No difference was present in saccade latency across the conditions. In both (C) and (D) the colored dots indicate Observer means/medians, and the error bars indicate the 95% CI.

Effect of distractor presence on saccade landing error

We examined whether saccade landing points were different in Distractor Present trials as compared to Distractor Absent trials. Observers landed, on average, 1.17° ($SD = 0.72$) from the saccade target in the Distractor Absent condition. In the Distractor Present condition, we observed an average landing error of 2.89° ($SD = 1.50$). The landing error was higher in the Distractor Present trials as compared to the Distractor Absent trials, $BF_{10} = 4.24 \times 10^{10}$, 95% CI [1.57 to 1.85] (Figure 5A). Next, we investigated whether saccades landed in-between the target and the distractor in the Distractor Present trials, or saccades got less precise

overall in the Distractor Present condition. To this end, we compared the mean polar angle of saccades in the Distractor Present and Distractor Absent conditions, where the target is presented at a polar angle of 30° and the distractor at a polar angle of 60° . In the Distractor Absent condition, observers made saccades with an average polar angle of 30.1° ($SD = 4.97$). In the Distractor Present condition, this average was 44.8° ($SD = 10.28$). A Bayesian t test revealed that saccades in the Distractor Present condition were angled more towards the distractor as compared to the Distractor Absent condition, $BF_{10} = 8.45 \times 10^{14}$, 95% CI [14.12 to 15.23]. These findings are indicative of a

Model parameters	Landing distance is distractor present versus distractor absent		Landing distance is a continuous measure	
	BF ₁₀	Error	BF ₁₀	Error
Color change + observer	1.01×10^{673}	1.35%	1.01×10^{673}	1.07%
Distractor present/landing distance + observer	0.028	1.14%	0.18	1.23%
Color change + distractor present/landing distance + observer	3.02×10^{671}	2.92%	5.02×10^{671}	4.49%
Condition * distractor present/landing distance + observer	3.89×10^{670}	5.92%	5.22×10^{670}	1.62%
Observer	1.00	<0.01%	1.00	<0.01%

Table 2. Parameter estimates for Bayesian Model Averaging analysis investigating how saccade landing distance affects reported color across Color Change/Constant conditions. *Notes:* In the left column, landing distance is the comparison between distractor present versus distractor absent trials; in the right column, landing distance is a continuous measure of saccade deviation relative to the center of the saccade target. The * symbol denotes a model with both main effects and interaction effects between the parameters. Bayes Factors have been rescaled to the random effects model (Observer only) for readability.

global effect, confirming the successful manipulation of saccade landing point by presenting a distractor, and increasing the average distance to the target from 1.17° to 2.89°.

Effect of saccade landing point on color reports

Next, we examined the reported hue across the different conditions. To recapitulate, a response of 0° would mean an observer reported the target hue exactly. In the Color Change condition a reported hue of 30° represents the target hue of the postsaccadic color.

The mean reported hue, with respect to the presented hue, in the Distractor Absent/Color Constant trials was -0.86° ($SD = 2.66$). In the Distractor Present/Color Constant condition observers reported a hue of -1.54° ($SD = 3.44$). Lastly, on average, observers reported a hue of 26.87° ($SD = 1.75$) in the Distractor Absent/Color Change condition, and a hue of 27.5° ($SD = 2.3$) in the Distractor Present/Color Change condition (see Figure 5C). A Bayesian model averaging analysis (parameter estimates are shown in Table 2) shows evidence for the inclusion of the factor Color Change to predict reported hue, $BF_{10} = 1.52 \times 10^{73}$. We observed no main effect of Distractor Presence on reported color, $BF_{01} = 19.78$. Lastly, we observed evidence against inclusion of interaction effect between Distractor Presence and Color Change, $BF_{01} = 1,067$. These results indicate that observers reported a different color in the Color Change condition, but this response was not affected by the presence of a distractor.

To examine the effect of landing position in more detail, we analyzed color performance in relation to Landing Error (as a continuous measure), rather than Distractor Presence (dichotomous). Landing Error was defined as the Euclidian distance between saccade landing point and midpoint of the target (x axis in

Figure 5B). With a Bayesian Model Averaging analysis, we found evidence that models including Color Change as a fixed effect outperformed models that did not $BF_{10} = 1.35 \times 10^{73}$. We observed that models that included the factor Landing Error performed worse, $BF_{01} = 12.12$. Lastly, the interaction between Color Change and Landing error was not significantly predictive of the reported color, $BF_{01} = 814.83$. Together, these analyses show that observers did not respond differently in the presence of a distractor that caused the eye to land far from the saccade target.

Control analysis: Reporting color mixtures

Next, we examined whether observers were reporting a mix of the pre- and postsaccadic colors in the Color Change condition, rather than only the postsaccadic color. In the Color Change condition observers were answering significantly different from both the postsaccadic color, $BF_{10} = 16.9$, 95% CI [24.5 to 29.5], and the presaccadic color $BF_{10} = 2.1 \times 10,702$. Participants are responding accurately; as in the Color Constant condition, we find that observers are reporting the target hue, $BF_{01} = 3.1$, 95% CI = $[-3.54$ to $1.46]$. Lastly, because we observed a slight counterclockwise bias in the Color Constant condition (reports $< 0^\circ$), we directly compared the Color Constant and the Color Change conditions. A comparison between conditions showed that the reported color in the Color Change condition deviated more from the postsaccadic color than the reported color in the Color Constant condition deviation from the presaccadic target color, $BF_{10} = 3,233$, 95% CI [1.09 to 2.71]. We conclude that changing the color of the saccade target during the saccade significantly affects the reported color, to a color that is in-between the presaccadic and postsaccadic color.

Control analysis: Saccadic latency

We examined whether saccade latencies differed across conditions, as differences in presaccadic exposure to the stimulus may affect the weights of the reported mixture color. The median saccade latency across conditions was 159 ms (IQR 142–175; see Figure 5D). We ran a Bayesian Model Averaging analysis, with Color Change and Distractor Presence as fixed effects and Saccade Latency as dependent variable. We found no main effect for Color Change, $BF_{01} = 13.41$, no main effect for Distractor Presence, $BF_{01} = 22.43$, and no interaction effect between Color Change and Distractor Presence, $BF_{01} = 4,920,867$. Thus, saccade latencies were the same across conditions.

Discussion

In the current study, we set out to investigate whether and how trial-by-trial deviations in saccade landing point affect transsaccadic feature perception. Saccade landing points naturally slightly deviate from the intended target location. Observers remain unaware of these deviations, allowing for continuous visual perception. From prior research it is clear that the position of visual information with respect to the eye affects the reliability of perceptual information (Oostwoud Wijdenes et al., 2015). Therefore, one could reason that deviations in saccade landing point would cause similar alterations in reliability of visual input. In Experiment 1, we investigated how saccade landing point affected integration of feature information across saccades (i.e., combining pre- and postsaccadic visual input) in terms of shifts in the mean reported color and a reduction of variance (similar to prior studies; Ganmor et al., 2015; Oostwoud Wijdenes et al., 2015; Wolf & Schütz, 2015). Saccade landing point did not affect bias and precision of the reported color. Even when landing far away from a saccade target, observers did not report a different color, presumably because these deviations were not affecting the postsaccadic reliability of the visual input.

We investigated color reports with an optimal observer model. We calculated the (statistically) optimal weights in combining presaccadic and postsaccadic information, to utilize both pre- and postsaccadic visual input to its fullest extent (Battaglia, Jacobs, & Aslin, 2003; Ganmor et al., 2015; Wolf & Schütz, 2015). In line with prior research, we found that observers were generally overweighing the foveal/postsaccadic visual input (Ganmor et al., 2015; Wolf & Schütz, 2015). We replicated the finding that observers' behavior is close to, but not quite, statistically optimal. However, whether transsaccadic feature integration really is a process that follows optimal Bayesian cue

integration is difficult to say, given that we could not compare observed percepts with optimal percepts for different stimulus reliabilities as we did not use degraded postsaccadic stimuli in the current study. In general, it seems that observers are somewhat predisposed to weigh foveal input more strongly than what would be predicted from the reliability. This is similar to multisensory perception in which the (more spatially reliable) visual input is overweighed relative to the auditory (less reliable) input (Alais & Burr, 2004; Battaglia et al., 2003; Rohe & Noppeney, 2016). Importantly, the optimal observer models allowed us to investigate whether observers weigh pre- and postsaccadic information differently across larger deviations in saccade landing point. These analyses showed that observers did not weigh presaccadic and postsaccadic information differently across saccadic landing positions, even when landing further away from the saccade target.

In Experiment 2 we set out to increase deviations in saccade landing point beyond the deviations that are observed when making a saccade to a single target (like in Experiment 1). To this end, we presented a distractor at the same time as the colored target. As expected, saccades in trials in which both a distractor and a target were present landed in between the target and the distractor. We investigated the effect of saccade landing point on color reports in distractor present trials. Even under the relatively large saccade landing point deviations in Experiment 2, we found that color reports did not differ between saccades that landed closer to as compared to further away from the saccade target. This finding is striking as cone density drops off steeply with increasing distance to the fovea (Curcio et al., 1990). Behavioral studies have shown that color perception declines steadily with increasing distance from the fovea, although color can still be perceived to some extent up to 50° in the periphery (Hansen, Pracejus, & Gegenfurtner, 2009). However, in our experiments, even though the color information of the (relatively small) target stimulus is located up to 6° from the high cone density area of the retina, it does not alter how observers weigh presaccadic and postsaccadic visual input.

The finding that color reports are unaffected by saccade landing point raises the question as to how the visual system is able to accomplish such stability. Prior studies have found behavioral evidence supporting a separation of intended and actual saccade landing point, showing that visual attention is not mandatorily coupled to the saccade landing point (Van der Stigchel & de Vries, 2015; Wollenberg et al., 2017). This may be especially useful when visual information needs to be sampled specifically at the intended saccade landing point, rather than the actual saccade landing point. In line with this proposed mechanism, one notable study

has found that by redirecting attention by presenting a salient presaccadic distractor, both saccade motor performance and integration of pre- and postsaccadic feature information was impaired (Stewart & Schütz, 2018). The authors conclude that attention may be a mechanism which facilitates or allows for transsaccadic feature integration. The critical difference with our study and the Stewart and Schütz (2018) study is that the distractor was presented at an unpredictable moment, thus involuntarily redirecting attentional resources to the distractor. In our experiment, it is likely that attentional resources are distributed across the target and distractor, and not necessarily redirected away from the saccade target. Our study adds that disparity between intended and actual saccade landing point can be as large as 6° visual angle without affecting transsaccadic perception, as long as attentional processes are not disrupted, underlining the remarkable stability of visual perception in the face of motor variance.

The current results complement the prior hypothesis that the distance to fixation affects the reliability of visual input. In the series of experiments by Oostwoud-Wijdenes et al. (2015) observers fixated further away from the colored targets, and fully intended to do so, causing no dissociation between point of fixation and visual attention. Therefore, in the previous study, attention (*and* the point of fixation) was deployed further away from the color targets, causing a decrease in the reliability of visual input. In the current set of experiments, the saccade deviations were relatively unnoticed by the observers, as attention was still deployed to the saccade target, even when the saccade landing point differed from the position in space where attention was deployed. The combined results from Oostwoud-Wijdenes et al. (2015) and the current study raise important implications when investigating transsaccadic perception: Both the actual and intended saccade landing point need to be taken into consideration when considering an experimental design.

In Experiment 1, we found a shift in bias, but no increased precision of color reports. Further investigating the optimal observer model revealed that observers could have, theoretically, combined pre- and postsaccadic information more optimally to reduce their error beyond the standard deviation that we measured. First, this may be due to a design limitation, where participants are reporting the color of the object on a color wheel. Here, we introduced some motor error on top of the existing sensory error, whereas prior studies implementing the optimal-observer model to study feature integration used a binary (unsped) response (e.g., Ganmor et al., 2015; Wolf & Schütz, 2015). We somewhat expected these results, as they are related to a necessary trade-off in experiment design when studying transsaccadic integration. To elaborate,

studies that found higher precision due to combining pre- and postsaccadic visual input used degraded postsaccadic stimuli (Ganmor et al., 2015; Wolf & Schütz, 2015). Likely, foveal visual perception is so rapid and accurate that reduction of error due to combining extrafoveal (presaccadic information) and foveal input does not typically occur outside of a controlled (psychophysical) environment where foveal visual input can be degraded (see Strasburger, Rentschler, & Jüttner, 2011). In the current study, we opted to *not* use degraded foveal stimuli. Degrading a visual stimulus necessitates a particularly large change in the stimulus content during the saccade. Therefore, when using degraded visual stimuli, observers will be aware that something is changing when they are making a saccade. We were concerned that degrading the postsaccadic color in Color Constant trials would affect awareness of the changing color in these trials. Prior studies have shown that observers are more likely to notice multiple changes, (e.g., location and feature) than single changes, and crucially, that these changes can affect object recognition (Poth & Schneider, 2016; Tas, Moore, & Hollingworth, 2012). Both Poth and Schneider (2016), and Tas et al. (2012) postulate that changes in objects can eliminate transsaccadic integration. Reducing the amount of time the stimulus is shown on screen postsaccadically would likely not influence the pre- and postsaccadic weights much, as postsaccadic visual input is weighed and processed immediately after the saccade (Wolf & Schütz, 2015). Furthermore, we were similarly restricted in not being able to change the position of the target, as it would (likely) break object correspondence. Here, we opted to use an experiment in which we were more likely to find integration in terms of mean shifts, than in terms of error reduction, while ensuring a lack of awareness of the changes in colors across conditions.

Lastly, we note that transsaccadic feature integration is a contentious topic, where many studies find limited or nonexistent transsaccadic feature integration (Jonides et al., 1983; Yao, Treue, & Krishna, 2016). This contentiousness within the literature of transsaccadic feature integration is especially striking when compared to the strong body of literature supporting the transfer of *spatial* information (attentional pointers) across saccades (e.g., Collins, Rolfs, Deubel, & Cavanagh, 2009; Rolfs & Szinte, 2016; Yao et al., 2016). At current, whether transsaccadic feature integration is indeed a literal transfer and mixing of features, or some other higher order process remains debated. It seems that feature integration may require congruence between signals, as shown in multisensory integration (Atkins, Fiser, & Jacobs, 2001; Parise, Spence, & Ernst, 2012). Similar conclusions on the stimulus specificity of transsaccadic feature integration are drawn from a study which shows that presaccadic (visual) motion

integration across the currently attended and predictively remapped locations, but only for congruent motion signals (Szinte et al., 2016). Importantly, earlier studies largely disproved the existence of transsaccadic fusion, using highly dissimilar spatial arrays (Jonides et al., 1983), whereas more recent studies seem to examine transsaccadic memory processes, using similar pre- and postsaccadic visual input (Ganmor et al., 2015; Oostwoud Wijdenes et al., 2015; Wolf & Schütz, 2015). With regard to memory-based transsaccadic feature integration, our study adds that is likely a process which is saccade landing point invariant, and is possibly facilitated or modulated by visual attentional processes. Lower order visual processes are typically more spatially selective, due to overall smaller receptive field sizes in earlier parts of the visual processing hierarchy (Smith et al., 2001). The lack of spatial selectivity in our study, and the requirement of congruence of the signal across saccades, can be seen as (moderate) support that transsaccadic feature integration is a higher order process (as in Hübner & Schütz, 2017). Furthermore, several studies report that spatial judgement tasks may rely on saccade execution (Jayet Bray, Bansal, & Joiner, 2015; Collins et al., 2009). From our findings that saccade landing point does not affect feature integration we suggest that transsaccadic feature integration may be a separate process from transsaccadic spatial judgements, where spatial information needs to be transferred across saccades.

In conclusion, in the current study we set out to investigate the effect of saccade landing point deviations on transsaccadic integration. As transsaccadic feature integration remains a somewhat contentious topic, we aimed to investigate how the parameters of a saccade may affect this process. We hypothesized that, if attentional deployment is separate from saccade landing point, then pre- and postsaccadic information is weighed and integrated similarly even when saccades deviate away from the saccade target. In line with this hypothesis, we found no indication that deviations in saccade landing point affected transsaccadic integration. The deviations induced were as large as 6° visual angle, but we presume that with much larger deviations in saccade landing point transsaccadic integration would be affected at some point. However, deviations of this magnitude would likely not occur under everyday viewing circumstances in healthy observers. Taken together, this study provides compelling evidence for the disparity between the intended saccade target (locus of attention) and the actual saccade landing point. Based on prior research, we speculate that this disparity is the results of two flexible remapping systems, one based on memory/attentional pointers and another which predicts motor execution. These mechanisms, separating attentional deployment from saccade execution, may very well underlie our

stable representation of the visual world, despite frequent deviations in saccade landing point due to oculomotor variation. It seems that these systems are so efficient in their interaction that stable perception can be facilitated outside the range of regular oculomotor variance, offsetting the lower acuity of postsaccadic visual input when a saccade deviates away from its intended target.

Keywords: saccadic eye movements, transsaccadic integration, global effect, visual attention

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References

- Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, 14, 257–262, [https://doi.org/10.1016/S0960-9822\(04\)00043-0](https://doi.org/10.1016/S0960-9822(04)00043-0).
- Atkins, J. E., Fiser, J., & Jacobs, R. A. (2001). Experience-dependent visual cue integration based on consistencies between visual and haptic percepts. *Vision Research*, 41, 449–461, [http://doi.org/10.1016/S0042-6989\(00\)00254-6](http://doi.org/10.1016/S0042-6989(00)00254-6).
- Battaglia, P. W., Jacobs, R. A., & Aslin, R. N. (2003). Bayesian integration of visual and auditory signals for spatial localization. *Journal of the Optical Society of America A*, 20(7), 1391–1397, <http://doi.org/10.1364/JOSAA.20.001391>.
- Boronine, A., & McGinley, R. (2017). HSLuv. Retrieved from <https://github.com/hsluv/hsluv-python>
- Burr, D. C., Morrone, M. C., & Ross, J. (1994, October 6). Selective suppression of the magnocellular visual

- pathway during saccadic eye movements. *Nature* 371(6497), 511–513, <http://doi.org/10.1038/371511a0>.
- 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://doi.org/10.1167/9.5.29>. [PubMed] [Article]
- Coren, S., & Hoenig, P. (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and Motor Skills*, 32(2), 499–508, <http://doi.org/10.2466/pms.1972.34.2.499>.
- Cronin, D. A., & Brockmole, J. R. (2016). Evaluating the influence of a fixated object's spatio-temporal properties on gaze control. *Attention, Perception, & Psychophysics*, 78(4), 996–1003, <http://doi.org/10.3758/s13414-016-1072-0>.
- Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, 292(4), 497–523.
- Dalmajer, E. S., Mathôt, S., & Van der Stigchel, S. (2014). PyGaze: An open-source, cross-platform toolbox for minimal-effort programming of eye-tracking experiments. *Behavior Research Methods*, 46(4), 913–921, <http://doi.org/10.3758/s13428-013-0422-2>.
- Deubel, H. (1995). Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Research*, 35(23–24), 3529–3540, [http://doi.org/10.1016/0042-6989\(95\)00058-M](http://doi.org/10.1016/0042-6989(95)00058-M).
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, 36(12), 1827–1837, [http://doi.org/10.1016/0042-6989\(95\)00294-4](http://doi.org/10.1016/0042-6989(95)00294-4).
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, 36(7), 985–996, [http://doi.org/10.1016/0042-6989\(95\)00203-0](http://doi.org/10.1016/0042-6989(95)00203-0).
- 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, <http://doi.org/10.1167/15.16.8>. [PubMed] [Article]
- Hansen, T., Pracejus, L., & Gegenfurtner, K. R. (2009). Color perception in the intermediate periphery of the visual field. *Journal of Vision*, 9(4):26, 1–12, <http://doi.org/10.1167/9.4.26>. [PubMed] [Article]
- He, D., Mo, C., & Fang, F. (2017). Predictive feature remapping before saccadic eye movements. *Journal of Vision*, 17(5):14, 1–12, <http://doi.org/10.1167/17.5.14>. [PubMed] [Article]
- Herwig, A. (2015). Transsaccadic integration and perceptual continuity. *Journal of Vision*, 15(16):7, 1–6, <http://doi.org/10.1167/15.16.7>. [PubMed] [Article]
- Hoeting, J., Maigan, D., Raftery, A., & Volinski, C. (1999). Bayesian model averaging. *Statistical Science*, 14(4), 382–401, <http://doi.org/10.1002/9781118445112.stat07874>.
- Hübner, C., & Schütz, A. C. (2017). Numerosity estimation benefits from transsaccadic information integration. *Journal of Vision*, 17(13):12, 1–16, <http://doi.org/10.1167/17.13.12>. [PubMed] [Article]
- Jayet Bray, L. C., Bansal, S., & Joiner, W. M. (2015). Quantifying the spatial extent of the corollary discharge benefit to transsaccadic visual perception. *Journal of Neurophysiology*, 115(3), 1132–1145, <http://doi.org/10.1152/jn.00657.2015>.
- Jonides, J., Irwin, D. E., & Yantis, S. (1983). Failure to integrate information from successive fixations. *Advancement Of Science*, 222(4620), 188.
- Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*, 90(430), 773–795.
- Klapetek, A., Jonikaitis, D., & Deubel, H. (2016). Attention allocation before antisaccades. *Journal of Vision*, 16(1):11, 1–16, <http://doi.org/10.1167/16.1.11>. [PubMed] [Article]
- Love, J., Selker, R., Marsman, M., Jamil, T., Dropmann, D., Verhagen, A. J., & Wagenmakers, E. J. (2015). JASP (Version 0.7)[computer software]. Amsterdam, the Netherlands: Jasp project.
- Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, 81(12), 899–917.
- Morey, R. D., & Rouder, J. N. (2015). BayesFactor: Computation of Bayes Factors for Common Designs.
- Morris, A. P., Liu, C. C., Cropper, S. J., Forte, J. D., Krekelberg, B., & Mattingley, J. B. (2010). Summation of visual motion across eye movements reflects a nonspatial decision mechanism. *Journal of Neuroscience*, 30(29), 9821–9830, <http://doi.org/10.1523/JNEUROSCI.1705-10.2010>.
- 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, <http://doi.org/10.1523/JNEUROSCI.1040-15.2015>.
- Paeye, C., Collins, T., & Cavanagh, P. (2017). Transsaccadic perceptual fusion. *Journal of Vision*, 17(1):

- 14, 1–11, <http://doi.org/10.1167/17.1.14>. [PubMed] [Article]
- Parise, C. V., Spence, C., & Ernst, M. O. (2012). When correlation implies causation in multisensory integration. *Current Biology*, 22, 46–49, <http://doi.org/10.1016/j.cub.2011.11.039>.
- Poth, C. H., & Schneider, W. X. (2016). Breaking object correspondence across saccades impairs object recognition: The role of color and luminance. *Journal of Vision*, 16(11):1, 1–12, <http://doi.org/10.1167/16.11.1>. [PubMed] [Article]
- R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rohe, T., & Noppeney, U. (2016). Distinct computational principles govern multisensory integration in primary sensory and association cortices. *Current Biology*, 26(4), 509–514, <http://doi.org/10.1016/j.cub.2015.12.056>.
- Rolfs, M., & Szinte, M. (2016). Remapping attention pointers: Linking physiology and behavior. *Trends in Cognitive Sciences*, 20(6), 399–401, <http://doi.org/10.1016/j.tics.2016.04.003>.
- Schut, M. J. (2018). P05: Transsaccadic integration is unaffected by saccade landing point, <http://doi.org/10.17605/OSF.IO/YZW5J>.
- Smith, A. T., Singh, K. D., Williams, A. L., & Greenlee, M. W. (2001). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cerebral Cortex*, 11, 1182–1190, <http://doi.org/10.1093/cercor/11.12.1182>.
- Stewart, E. E. M., & Schütz, A. C. (2018). Attention modulates trans-saccadic integration. *Vision Research*, 142, 1–10, <http://doi.org/10.1016/j.visres.2017.11.006>.
- Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *Journal of Vision*, 11(5):13, 1–82, <http://doi.org/10.1167/11.5.13>. [PubMed] [Article]
- Subramanian, J., & Colby, C. L. (2013). Shape selectivity and remapping in dorsal stream visual area LIP. *Journal of Neurophysiology*, 111(3), 613–627, <http://doi.org/10.1152/jn.00841.2011>.
- Szinte, M., Jonikaitis, D., Rolfs, M., Cavanagh, P., & Deubel, H. (2016). Presaccadic motion integration between current and future retinotopic locations of attended objects. *Journal of Neurophysiology*, 116(4), 1592–1602, <http://doi.org/10.1152/jn.00171.2016>.
- Tas, A. C., Moore, C. M., & Hollingworth, A. (2012). An object-mediated updating account of insensitivity to transsaccadic change. *Journal of Vision*, 12(11):18, 1–13, <http://doi.org/10.1167/12.11.18>. [PubMed] [Article]
- Van der Stigchel, S., & de Vries, J. P. (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. *Journal of Vision*, 15(15):17, 1–12, <http://doi.org/10.1167/15.15.17>. [PubMed] [Article]
- Van der Stigchel, S., Heeman, J., & Nijboer, T. C. W. (2012). Averaging is not everything: The saccade global effect weakens with increasing stimulus size. *Vision Research*, 62, 108–115, <http://doi.org/10.1016/j.visres.2012.04.003>.
- Van der Stigchel, S., & Hollingworth, A. (2018). Visuospatial working memory as a fundamental component of the eye movement system. *Current Directions in Psychological Science*, 27(2), 136–143.
- Van der Stigchel, S., & Nijboer, T. C. (2011). The global effect: What determines where the eyes land? *Journal of Eye Movement Research*, 4(2), 1–13, <http://doi.org/10.16910/jemr.4.2.3>.
- Wagenmakers, E.-J., Lodewyckx, T., Kuriyal, H., & Grasman, R. (2010). Bayesian hypothesis testing for psychologists: A tutorial on the Savage-Dickey method. *Cognitive Psychology*, 60(3), 158–189, <http://doi.org/10.1016/j.cogpsych.2009.12.001>.
- Wittenberg, M., Bremmer, F., & Wachtler, T. (2008). Perceptual evidence for saccadic updating of color stimuli. *Journal of Vision*, 8(14):9, 1–9, <http://doi.org/10.1167/8.14.9>. [PubMed] [Article]
- 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, <http://doi.org/10.1167/15.16.1>. [PubMed] [Article]
- Wollenberg, L., Deubel, H., & Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. *PLoS Biology*, 16(6):e2006548.
- Yao, T., Treue, S., & Krishna, B. S. (2016). An attention-sensitive memory trace in macaque MT following saccadic eye movements. *PLoS Biology*, 14(2), 1–17, <http://doi.org/10.1371/journal.pbio.1002390>.