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All is not lost: Post-saccadic contributions to the perceptual omission of intra-saccadic streaks

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ABSTRACT

Saccades rapidly jerk the eye into new positions, yet we rarely experience the motion streaks imposed on the retinal image. Here we examined spatial and temporal properties of post-saccadic masking—one potential explanation of this perceptual omission. Observers judged the motion direction of a target stimulus, a Gaussian blob, that moved vertically upwards or downwards and then back to its initial position, just as observers made a saccade. We manipulated the onset and offset of the target and of distractors in various spatial relations to the target, and assessed their effect on performance and subjective confidence. Although the presence of the target after the saccade caused the strongest omission, the offset of spatially distant distractor stimuli upon saccade offset also impaired performance. The temporal properties of these two separate effects suggest that, in addition to masking, an independent effect of attentional distraction further accentuates perceptual omission of intra-saccadic motion streaks.

1. Introduction

Our visual experience of the world is stable and continuous despite the frequent and large interruptions that blinking and eye movements cause to the retinal input. With saccadic eye movements, the puzzle of maintaining a stable experience is especially complex. Large eye movements create streaks of light across the retina that generally escape phenomenal visual experience. On top of this, visual information may be integrated across the displacements of the retinal image from one fixation to the next, such that perception remains continuous in real world spatial coordinates despite changes to retinal spatial coordinates. This description generates three distinct challenges for our understanding of visual processing around saccades: (1) Why do we lack awareness of the streaks created by saccadic eye movements, (2) Why do we not perceive the temporal gap in the visual input, and (3) How do we maintain perceptual stability in spatial coordinates (Bridgeman, Van der Heijden, & Velichkovsky, 1994; Rolfs, 2015). An ideal mechanism would account for all three of these challenges, but it is likely that a number of distinct mechanisms contribute. Detailed reviews and discussions of the many theoretical accounts of how a stable and continuous world can be maintained despite the disruptions caused by saccadic eye movements can be found in the seminal BBS paper by Bruce Bridgeman and his colleagues (Bridgeman et al., 1994), in Castet, Jeanjean, and Masson (2001) and the response of Ross and colleagues in the same issue (Ross, Morrone, Goldberg, & Burr, 2001), and more recently in Wurtz (2008). The experiments presented in this manuscript seek to

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explicate one such potential mechanism: backward masking.

Backward masking describes the reduced visibility of a target stimulus by the subsequent presentation of a 'mask' stimulus, presented to a participant during fixation (Kahneman, 1968; for reviews see Enns & Di Lollo, 2000; Breitmeyer & Öğmen, 2000, 2006; Bachmann, 2015). Based on this effect, typically observed during fixation, it has been suggested that the post-saccadic visual scene acts to backward mask the intra-saccadic retinal image, thereby creating saccadic omission, or a complete lack of awareness of intra-saccadic retinal stimulation. Indeed, a wealth of evidence suggests that simply removing post-saccadic input restores performance on a range of tasks involving perception during saccades (Campbell & Wurtz, 1978; Castet & Masson, 2000; Castet, Jeanjean, & Masson, 2002; Matin, Clymer, & Matin, 1972). Campbell and Wurtz (1978) found that by illuminating the observer's surroundings only during their saccades, observers were able to clearly perceive the retinal stimulation during saccadic eye movements – a blurred or 'greyed out' image of the observer's surroundings. However, if the room was illuminated for longer than 40 ms after the saccade, the brief 'grey out' was completely eliminated from their phenomenal perception.

The fact that there is 'grey out', caused by the rapid movement of the retinal image over slowly-integrating photoreceptors, may indeed be important for masking to occur. During fixation, Corfield, Frosdick, and Campbell (1978) found that the presentation of a blank grey screen, lasting as long as the duration of a saccade or more, could be eliminated from awareness if it was preceded and followed by a sinewave grating. High contrast patterns or lines could not be eliminated from awareness with these same masking stimuli. This evidence suggests that backward masking could limit the visibility of intra-saccadic retinal stimulation *in the same manner* as backward masking during fixation, with the exception that the stimulation around the time of the saccade is itself responsible for masking, as opposed to the specific experimental manipulation that occurs to induce masking during fixation. This comparison suggests that our understanding of visual perception around the time of a saccade can be enriched by what we know from backward masking studies during fixation. In turn, our understanding of the natural function of backward masking may benefit greatly from a potential relation to post-saccadic masking in active vision.

Extensive research into backward masking during fixation has detailed the complex relationship between the properties of the target and effective mask stimuli (see Breitmeyer & Öğmen, 2006). The most prominent of these properties is the temporal relationship between target and mask. The stimulus onset asynchrony (SOA) describes the time between target stimulus onset and mask onset. Target visibility varies substantially as a function of SOA and usually follows one of two functions: a non-monotonic U-shaped function, where visibility first decreases (up to around 30–70 ms) and then increases again with increasing SOAs; or a monotonic function, where visibility is poorest when the mask follows immediately after the target stimulus and then increases with increasing SOA (Bachmann, 1994; Breitmeyer & Öğmen, 2006). Effective saccadic omission of intra-saccadic stimuli requires a monotonic masking function, where the high-contrast, broadband spatial frequency retinal input immediately after the saccade strongly masks the streaky/smeared out retinal input during the saccade.

During fixation, the monotonic masking function is normally produced by a mask that spatially overlaps with a target (see Breitmeyer & Öğmen, 2006; Bachmann, 1994; though not necessarily retinally overlapping: McFadden & Gummerman, 1973). In some post-saccadic masking experiments, however, a rather sparse stimulus display is used and the simple removal of a small target stimulus by the end of the saccade is sufficient to allow for the perception of the streak of that target across the retina during the saccade (Matin et al., 1972; Deubel, Schneider, & Bridgeman, 1996, 2002; Bedell & Yang, 2001; Duyck, Collins, & Wexler, 2016). In these cases, the target had *masked itself* in neither the same retinal nor spatial location, which is unlike backward masking during fixation. For example, Duyck et al. (2016) found the intra-saccadic smear of a small LED could be masked by the presence of a similar LED after the saccade, located up to 6° away from the static target. Thus, the masking of intra-saccadic retinal stimulation could be more complex than is suggested by studies of backward masking during fixation. Put differently, the post-saccadic retinal input may reduce intra-saccadic omission in more ways than just those captured by traditional backward masking.

Although in natural environments a high-contrast, full field mask impinges on the retina after each saccade, it remains unclear which properties of this input give rise to saccadic omission. The systematic investigation of interactions between post-saccadic stimuli and intra-saccadic retinal input can provide insight into the processing of visual information during saccades. The following experiments therefore seek to examine the spatial and temporal relationships between intra-saccadic motion streaks and post-saccadic visual information. We created an objective discrimination task by moving a full contrast Gaussian blob either up or down and back to its original location during saccadic eye movements (Fig. 1a). Previous literature suggests that the streak of the stimulus will be clearly visible if that stimulus is removed from the screen before the end of the saccade (Duyck et al., 2016; Bedell & Yang, 2001; Deubel et al., 1996, 2002; Matin et al., 1972). Full masking of the intra-saccadic retinal input would mean that intra-saccadic stimulation does not yield a conscious percept, and performance in the task would be at chance level. We then manipulated the temporal and spatial relations of target and mask stimuli to examine the specific constraints for effective saccadic omission (Fig. 1b and c). First, we sought to replicate the effect of a reduction in performance when the target remains on screen after the end of the saccade. Second, we manipulated the presence of the additional distractor stimuli before, during, and after the saccade to examine at what time the presence, or onset, of other stimuli reduced performance. That is, could omission be elicited by stimuli occurring during the saccade, or only those appearing after, or some specific combination? Third, we investigated whether performance in the task was affected by the distance of the post-saccadic distractors to the target in terms of both real world spatial coordinates and retinal coordinates, by manipulating the location of the distractor stimuli relative to the target stimulus and the direction of the saccade. We specified four distractor locations: a 'close' distractor that was just outside the end of target movement, a 'far' distractor that should not affect performance if spatial proximity is necessary, as well as 'inside' and 'outside' distractors, where the 'inside' distractor would be close to the retinal streak of the target stimulus but the 'outside' distractor would not, to test whether proximity to the retinal trace of the target is important (Fig. 1c).

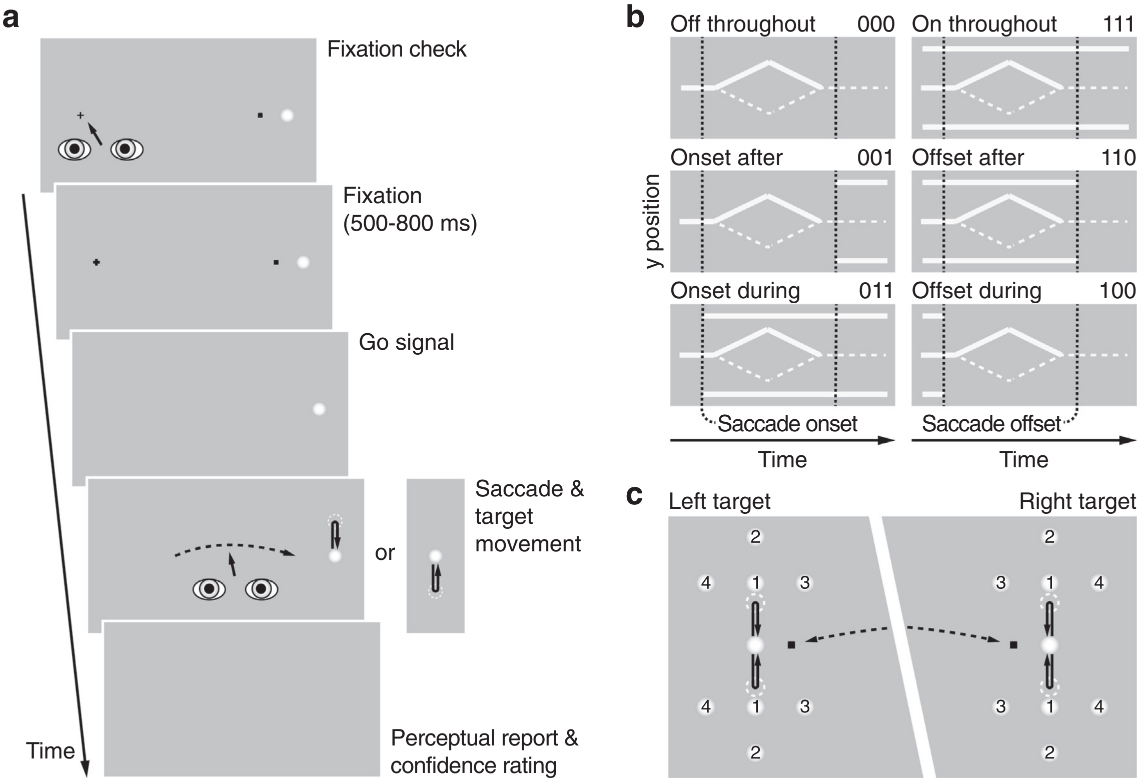

Fig. 1. Methods. (a) Trial procedure of an example trial with a left-to-right saccade and only the target stimulus (no distractors). At the start of each trial the fixation cross, landing point and target stimuli were visible (as well as distractors in a subset of the conditions). When fixation was recognised (eye tracker detects the eyes within 1.5° of the fixation cross) the fixation cross increased in size and the fixation time began. After a variable fixation time (500–800 ms), the saccade was cued by the disappearance of the fixation and landing points (only the stimuli remain on the screen; here, just the target stimulus). The observer begins a saccade to the remembered location of the landing zone, and once their saccade is detected, the target moves vertically 4° up or down and back to its original location, over 30 ms. A blank screen then prompts the observer's perceptual response and confidence rating. (b) Distractor timing. The x-axis shows time relative to the saccade. The central white line depicts the target stimuli which moves either up or down and back to centre during the saccade, and then is either removed by the end of the saccade, or remains on screen. The distractor stimuli are depicted by the white lines above and below the target. There were six timing conditions which can be represented by the presence of the distractor before, during, and after the saccade: 000 – off throughout; distractor appears after the saccade: 001 – onset after; distractor appears at the start of the saccade and remains: 011 – onset during; distractor is on screen the whole trial: 111 – on throughout; distractor is on at the beginning of the trial but removed by the end of the saccade: 110 – offset after; distractor is on at the beginning of the trial and removed as soon as the saccade is detected: 100 – offset during. (c) Distractor positions for a left-to-right saccade (right) and a right-to-left saccade (left). The target stimulus is shown in the centre, where the possible movement end points are marked with the dotted white circles. In the near condition (marked with 1), the distractors sit 5.5° above and below the original target location (adjacent to the extremes of the target movement). In the far condition (2), the distractors are 9.5° from the original target location. The inside (3) and outside (4) distractors are 5.5° vertically and horizontally offset from the original target location.

2. Experiment 1

2.1. Material and methods

2.1.1. Participants

Ten observers were recruited through word of mouth and campus mailing lists. They had normal or corrected-to-normal vision and gave informed consent prior to beginning the experiment. Monetary reimbursement was offered for their time (a total of 25 € after the completion of all sessions). One participant was unable to complete a sufficient number of trials, and one participant demonstrated outlier performance, and so eight participants were included in the final analysis (more details below). The study was conducted in agreement with the latest version of the Declaration of Helsinki; it has been preregistered on the Open Science Framework (OSF; https://osf.io/h56uj/).

2.1.2. Apparatus

Stimuli were projected onto a 200 × 113 cm video-projection screen (Celexon HomeCinema, Tharston, Norwich, UK), using a Propixx Projector (Vpixx Technologies, Saint-Bruno, QC, Canada) running at 1440 Hz, with a background luminance of 30 cd/m^2 and a resolution of 960 × 540 pixels[2]. Observers sat 270 cm from the projector with their head supported by a chin rest. Eye movements were monitored using an Eyelink 2 head-mounted system (SR Research, Osgoode, ON, Canada) with a sampling rate of 500 Hz. Stimulus display was controlled via MATLAB (Mathworks, Natick, MA, USA), using the PsychToolbox (Brainard, 1997; Kleiner et al, 2007; Pelli, 1997) and the Eyelink toolbox (Cornelisen, Peters, & Palmer, 2002) extensions, running on a Dell Precision T7810 Workstation with a Debian 8 operating system. Responses were collected via a standard keyboard.

2.1.3. Stimuli

The target stimulus was a full-contrast Gaussian blob subtending 3 degrees of visual angle (°) with a standard deviation of 0.5°, displayed on a grey background (mean luminance 30 cd/m^2). During fixation, the target stimulus was horizontally separated from the saccade landing point by 3°, outside the saccade path. The target stimulus was moved when saccades were in mid-flight, as described further below. Two distractor stimuli, identical to the target stimulus, were also employed. The location of distractor stimuli was manipulated across trials, as outlined further below.

2.1.4. Procedure

On each trial, the observer was asked to fixate on a fixation cross (0.5°). After a variable fixation duration (500–800 ms) they were cued, by the disappearance of the fixation cross and landing point, to make a saccade to the landing point specified by a small (0.5°) square displayed at a horizontal distance of 16°. Once the beginning of the saccade was detected, the target stimulus (displayed from the start of the trial) was moved vertically 4° either up or down, and then back to its original location, over a duration of 30 ms (to be completed by the end of the saccade). The high refresh rate of the projector allowed for 43 frames to describe the target motion over 30 ms, as such the target was moved at 0.186° per frame in screen coordinates and about 0.29° per frame in retinal coordinates (at saccadic peak velocity of about 395° per second), creating relatively smooth motion. The observer was then asked to decide whether the stimulus moved up or down from its original location, using the up and down arrow keys. Following their response, observers gave a rating of how clearly they perceived evidence of stimulus movement, ranging from 1 (no perception) to 3 (clear perception). This procedure is outlined in Fig. 1a.

The experiment began with a practice block of 40 trials to familiarise the participant with the procedure and to ensure they were able to perceive the motion streaks under optimal conditions. In these practice trials, the target stimulus was present from the beginning of the trial and removed before the completion of the saccade (after target movement was complete), while no distractor stimuli were presented. After each practice trial, observers received visual feedback as to whether their response was correct.

The main experiment manipulated three variables: (1) the duration of the target stimulus (either disappearing before the end of the saccade, or remaining on screen for approximately 400 ms after the saccade), (2) the onset and offset of distractor stimuli (six conditions, described further below), and (3) the location of the distractor stimuli (four conditions, also described further below). The onset and offset of the distractor stimuli was controlled relative to the saccade; appearing before the saccade, with saccade onset or upon saccade offset, and disappearing either with saccade onset, with saccade offset, or after the saccade, forming six conditions (Fig. 1b). For brevity, we labeled these conditions according to whether the target was present or not before, during, and after the saccade with a 1 or a 0 in each of the three digit locations respectively. These conditions are as follows: no distractor stimuli before, during, or after [off throughout: 000]; distractors appearing around the end of the saccade once target movement is complete, and remaining on screen [onset after: 001]; distractors appearing at the start of the saccade and remaining on screen [onset during: 011]; distractors remaining on screen for the whole trial [on throughout: 111]; distractors present at the start of the trial and removed by the end of the saccade once target movement is complete [offset after: 110]; distractors present at the start of the trial and removed at the beginning of the saccade [offset during: 100]. Distractors were presented in one of four sets of locations (Fig. 1c): (1) 5.5° vertically above and below the target stimulus (near condition, just past the end of stimulus movement), (2) 9.5° vertically above and below the target stimulus (far condition), (3) 5.5° above/below and toward the fixation cross (7.8° diagonally inward conditions), or (4) 5.5° above/below and away from the fixation cross (7.8° diagonally outward condition). These timing and location conditions were fully counterbalanced and randomly interleaved across trials.

In addition to the above variables, the direction of the saccade (horizontally 16° left or right) and the direction of the target stimulus motion (vertically 4° up or down) was also fully counterbalanced and randomly interleaved across trials. The position of the fixation and landing points was randomly jittered from trial to trial by a radius of up to 1° (while maintaining equal y-positions and a horizontal distance of 16° between fixation and landing). We attempted to collect around 48 trials per participant, per condition combination, resulting in a total of 2304 trials, which were collected over three sessions of approximately one hour each.

Eye movements were tracked throughout each trial, with online assessment of fixation, saccade detection, and landing zone. The fixation duration began once the tracker detected the eyes were within 1.5° of the fixation cross, and the eyes had to reach the landing zone (2° from the landing point) for the trial to be considered valid. Online detection of saccades was conducted using a velocity-based algorithm, as described by Engbert and Mergenthaler (2006). A saccade was detected once four consecutive x/y eye-position samples exceeded the threshold velocity (the median velocity plus ten times the standard deviation of samples collected since the beginning of the current fixation) after the saccade was cued. Trials were discarded (and repeated pseudo-randomly amongst future trials) if the eyes did not reach the landing zone, or if more than one saccade was detected between the saccade cue and reaching the landing zone. One participant had trouble making saccades of sufficient amplitude and produced less than one session of valid trials over the first two sessions, so testing was aborted and the participant's data was excluded from further analysis (as noted under *Participants*).

2.1.5. Analysis

Eye tracking: Eye tracking data was first analysed to remove any trials where the eye-movement did not match the required trial protocol: the saccade must be of sufficient length (16 ± 2°), only one saccade can be made per trial to reach the landing zone, the target stimulus must begin moving after the start of the saccade and stop before the end of the saccade, and trials where distractor stimuli were to be removed before the end of the saccade must also meet this condition. Saccades were detected using a median-velocity based algorithm implemented in Matlab, based on the x/y eye positions recorded by the eye tracker (Engbert & Mergenthaler, 2006).

Performance: Following the removal of invalid trials, each observer's proportion of correct responses was calculated for each condition combination. Within-subject confidence intervals were calculated as per Loftus and Masson (1994). The impact of experimental factors (fixed effects) and individuals (random effects) were then assessed using General Linear Mixed Effect Models (GLMM).

GLMM modelling: Logistic mixed effects regressions were used to assess the direction and extent of the effect of experimental factors on performance. We not only wished to assess the significance of effects, but also their most parsimonious description. Thus, we fit several models and compared them using the Bayesian Information Criterion (BIC) and relevant Bayes Factors (BF; Wagenmakers, 2007). We considered three descriptions of distractor distance and five descriptions of distractor timing, as well as whether these effects should be included at all (further description below). Fixed effects were coded for treatment contrasts, where each condition was compared to what could be considered a 'null' condition (target absence for the target duration conditions, and distractor absence for the distractor conditions). Participant ID was included as a random intercept (no slope). Logistic mixed effects regressions were fit in R (R Core Team, 2017), using lme4 (Bates, Mächler, Bolker, & Walker, 2015).

Confidence ratings: Observers' confidence ratings were also used to confirm the influence of the distractors and target stimulus duration on the perception of intra-saccadic motion streaks. The proportion correct scores from trials within each confidence rating (regardless of condition) were used as a 'sanity check', where proportion correct was expected to increase with increasing rating. Proportion confidence was then calculated by averaging over the ratings transformed to the range 0:0.5:1 and the proportion confidence was compared across conditions.

2.2. Results

After examining the overall proportion correct, one additional participant was removed from further analysis (as noted under *Participants*). Unlike the other participants, average performance was below chance at 41% correct (over a total of 2240 valid trials), and performance tended to decrease with increasing confidence ratings, suggesting that the participant may have been attempting to rely on an invalid cue. The remaining eight participants entered the analysis. Their data were cleaned to remove any trials that did not meet the criteria, as described in the Analysis section. After removing trials, there was an average of 44.8 (SD = 4.6) trials per condition combination, per observer. The average saccade duration was 61.7 ms (SD = 4.1 ms), and on average the target stimulus movement began 15.3 ms (SD = 3.4) after the start of the saccade, and ended 15.1 ms (SD = 7.3) before the saccade was completed; the full distributions are shown in Fig. 2.

Fig. 3 shows proportion correct as a function of condition. Irrespective of the distractor stimuli, performance was consistently better when the target stimulus was removed before saccade offset (0 ms), compared to when it remained on the screen after saccade

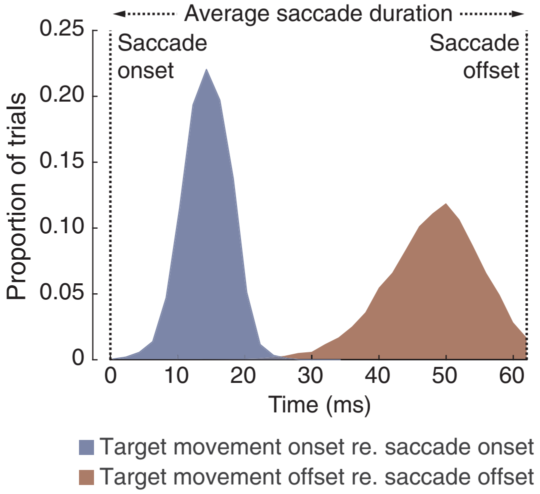

Fig. 2. Distribution of target timings relative to the saccade. The blue distribution shows the proportion of trials where the target started moving at each time point relative to the start of the saccade. The red distribution shows the proportion of trials where the target finished movement at each time point relative to the end of the saccade (shown relative to the average saccade duration). Trials were removed if target movement was not completed by the end of the saccade, hence the lack of saturation toward the end of the saccade. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

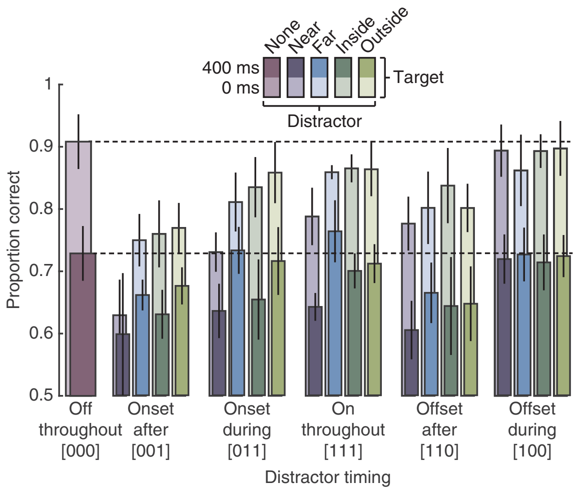

Fig. 3. Proportion of correct reports in each condition. The lighter bars show performance when the target was removed before the end of the saccade (Target 0 ms), whereas the darker bars show performance when the target remained on the screen for 400 ms after the saccade (Target 400 ms). The wider purple bars show the proportion correct when no distractors were present, providing a reference for all other conditions (dashed horizontal lines). Error bars indicate 95% within-participant confidence intervals. The distractor timing conditions are labeled as in Fig. 1b, where 1 indicates the presence of the distractor (or 0, the absence) before, during, and after the saccade in each digit location, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

offset (400 ms). Certain distractor conditions appeared to further reduce performance compared to when no distractors were present (000), however, the extent of their impact on performance appeared to interact in a complex way with their spatiotemporal characteristics. We used Generalised Linear Mixed Models (GLMMs) to establish these influences.

We fit a total of twelve models to find the most parsimonious account of the observed differences in performance. First, a null model was fit that included participants as a random effect, but no fixed effects. This was compared to a full model, with three fixed effects: target duration (0, 400 ms), distractor location (absent, near, far, inside, outside), and distractor duration (absent, and the five conditions described above). There was very strong evidence that the full model provided a better description than the null (BF = $5.02e^{113}$, computed from BIC values shown in the top two boxes of Fig. 4), indicating that the experimental manipulations of the target and distractor stimuli had some effect on performance.

Next, we sought the most parsimonious description of the experimental manipulations by a process of model minimization. We first compared simplified descriptions of each of the fixed factors, in what was otherwise a full model. For distractor distance (Distance models in Fig. 4), we obtained strong evidence that the far, inside, and outside distractor conditions could be described as one mid/far condition, which was a better description than the full model (BF = $3.52e^{37}$) and better than having a mid (inside/outside distractors) and far condition separate (BF = $5.45e^{19}$). For the effect of distractor timing (Timing models in Fig. 4), we compared several ways to describe the conditions: presence during the saccade, presence after the saccade, whether there was an onset signal after the saccade, and an additional model that also included the offset signal with the onset signal, such that both contributed a single effect of a change around the end of the saccade. The onset signal model was a far better description of the effect of distractor timing than the models describing the effect as presence during or after the saccade. Furthermore, we obtained strong evidence that grouping both onset and offset conditions as a single effect of a change around the end of a saccade provided an even better fit to the data than the onset signal alone (BF = 4.99).

Finally, we fit a revised full model that included the most parsimonious descriptions of the distractor effects, and fit another three models to compare whether these effects could be left out altogether: one with no distance effect, one with no timing effect, and a model with only target duration as an effect (Simplified Models in Fig. 4). BFs provided very strong evidence that the full model with the more parsimonious descriptions of the effects was a better description of the data than the fullest model (BF = $1.69e^{42}$) and a better description than any of the simpler models (compared to the next lowest BIC, the No distance model: BF = $4.79e^{4}$).

The most parsimonious description of how intra-saccadic motion streak perception was affected by the presence of distractors (i.e., relative to the target only conditions) is shown in Fig. 5a. The estimated fixed effects and associated confidence intervals (Table 1) suggest a significant negative effect of target duration on performance. Distractors also had a significant negative effect on performance. Their impact decreased with distance (from near to mid/far) and was due to the onset/offset signal at the end of the saccade, rather than their mere presence at any point in time relative to the saccade. Further, we obtained a significant interaction between target duration and distractor effects: distractors had a subtler impact on performance when the target remained on screen for 400 ms after the end of the saccade. There were no interactions between distractor location and distractor timing, nor was there a three-way interaction between target duration and distraction location and timing.

An additional analysis was conducted to ensure that the differences in performance observed over experimental conditions could not have been mediated by differences in saccade amplitude (Stevenson, Volkmann, Kelly, & Riggs, 1986). First, summary statistics confirmed that average saccade amplitudes differed very little over the conditions (mean amplitude was 17.76°, SD = 1.5°, with

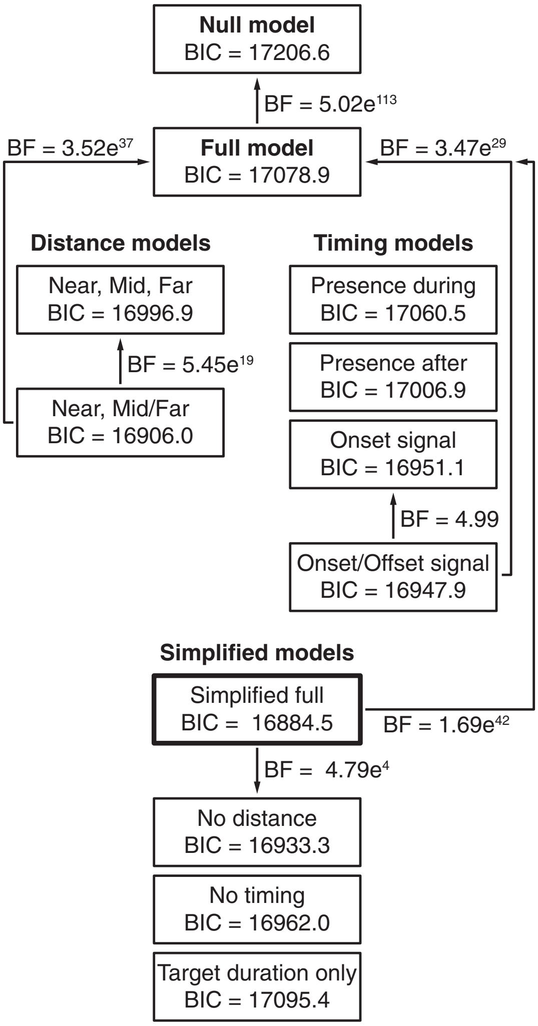

Fig. 4. Comparison of statistical models of observers' performance. We calculated BF_{01} as $e^{\left(\frac{BIC1-BIC0}{2}\right)}$. Arrows indicate the direction of comparison (point from BIC_1 to BIC_0). The top two boxes show the full and the null model, respectively. Boxes on the left show Distance models which provide simpler descriptions of the distractor locations. Boxes on the right show Timing models that use simpler descriptions of distractor timing. At the bottom, we show Simplified models that combine the most parsimonious descriptions of the effects.

means in each distractor condition ranging from 17.51° to 17.79°). Second, a general linear model of performance, with (normalized) saccade amplitude as a fixed effect and participant as a random effect showed only a small effect of saccade amplitude on performance (estimate: -0.06 ± 0.05, suggesting that a 1.5° increase in saccade amplitude would predict a 6% decrease in performance). However, this influence of saccade amplitude on performance did not vary with condition: When we fitted the best model of performance to saccade amplitudes (where some effect of condition would be observed if saccade amplitude varied predictably with the conditions that predicted performance), no significant effect of condition on saccade amplitude was found (the confidence intervals of all estimates of effects overlapped with zero). Thus, saccade amplitude can influence performance, but differences in saccade amplitude cannot explain the differences in performance observed across conditions.

Fig. 5b shows the proportion confidence across the model conditions. Confidence paralleled the results we obtained for performance across conditions, suggesting that lower performance was the result of observers not clearly perceiving the stimulus, rather than lapses or some post perceptual decision-making effect. Indeed, observers' confidence was well calibrated to their performance, with reported guesses (confidence of 1) showing performance near chance and reports of clear perception (confidence of 3) showing performance near ceiling (Fig. 5c).

3. Interim discussion

The experimental results suggest that the perception of intra-saccadic motion streaks can be interrupted not only by post-saccadic masking from the target stimulus, but also from distractor stimuli. Unlike the masking effect of the target stimulus, the mere presence

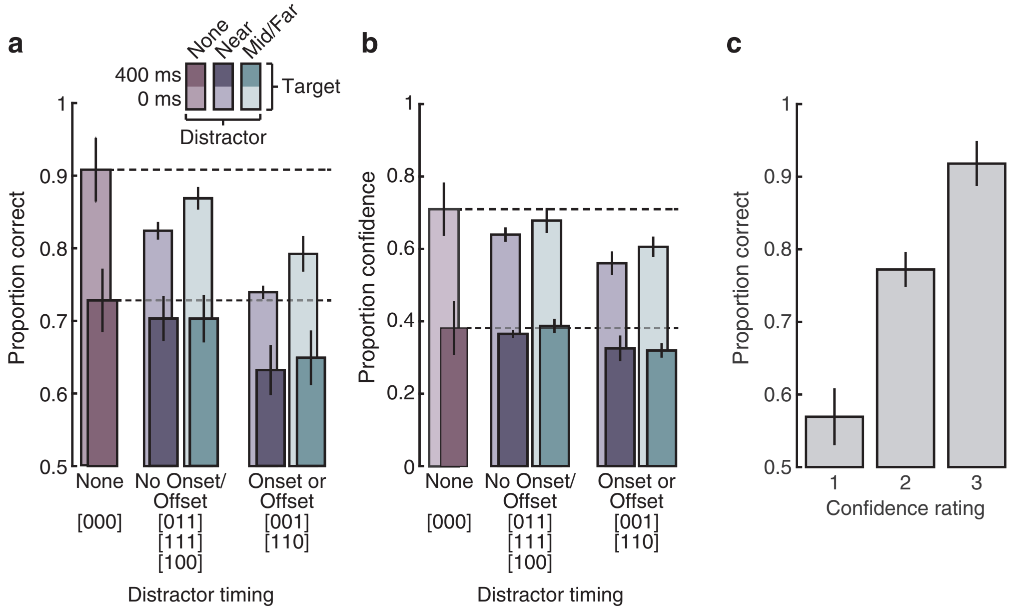

Fig. 5. Average proportion correct (a) and proportion confidence (b) according to the most parsimonious model descriptions. The distractor timing was most parsimoniously described by whether there was a change (an onset or offset signal) around the end of the saccade. The locations were most parsimoniously described by grouping the inside, outside, and far distractors into one mid/far group. Conventions as in Fig. 3. (c) Average proportion correct by confidence rating. Error bars show 95% within-participant confidence intervals. A confidence rating of 1 corresponded to 'just guessing', while 3 indicated 'clear perception'.

Table 1

Estimates of fixed effects from the most parsimonious model. A negative effect describes a decrease in performance relative to the contrasts (target removed before saccade offset and no distractor conditions for the target and distractor effects respectively). Along with the within-participants confidence intervals from the raw proportion correct scores shown in Fig. 5, confidence intervals presented here indicate significance (if they do not include 0).

Effect	Estimate	Lower CI	Upper CI
Intercept	2.519	1.991	3.046
Target duration (400 ms)	−1.408	−1.630	−1.187
Distractor near	−0.952	−1.196	−0.709
Distractor mid/far	−0.519	−0.731	−0.307
Distractor onset/offset	−0.550	−0.700	−0.401
Target duration (400 ms) × Distractor near	0.626	0.323	0.929
Target duration (400 ms) × Distractor mid/far	0.450	0.193	0.707
Target duration (400 ms) × Distractor onset/offset	0.226	0.032	0.420
Distractor location × Distractor Timing	−0.070	−0.345	0.205
Target duration × Distractor location × Distractor Timing	0.041	−0.324	0.407

of the distractors was less effective at impairing performance than an onset or offset signal around the time of end of the saccade. Even the offset of a distant stimulus can negatively affect performance (see Figs. 3 and 5a). Observers' confidence ratings suggest that these effects are perceptual in nature — observers are also less likely to report that they perceived the intra-saccadic motion streak under these conditions.

These data tell a somewhat different story from what has been suggested in the literature. The mere presence of the target after the saccade effectively—but not entirely—masks the stimulus during the saccade. That we observed less effective backward masking than previous experiments could be explained by several factors. When a large or full field stimulus/mask is used, intra-saccadic perception does tend to be completely omitted (Campbell & Wurtz, 1978; Castet & Masson, 2000; Castet et al., 2002). Moreover, since our task was deliberately quite easy, the intra-saccadic motion streak would need to be practically completely masked to produce a reduction in performance. In previous studies, in contrast, the task may have become impossible with even a slight degradation of intra-saccadic perception (e.g., Duyck et al., 2016).

The question of the spatial relation between the target and mask is an interesting one. Typically, in masking studies conducted during visual fixation, the mask is most effective when overlapping the stimulus (Bachmann, 2015). Non-spatially overlapping stimuli can act as masks in the case of object substitution masking, where the onset of target and mask is simultaneous but the offset of the mask trails that of the target (Enns & Di Lollo, 1997, 2000). However, this type of masking requires that observers are not attending the target, and is most effective with many possible targets (Enns & Di Lollo, 1997). In the present experiment, observers were almost certainly attending the target: It was the center of the perceptual task and always displayed close to the movement goal, where attention is allocated at the time of saccade onset (e.g., Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Ohl, Kuper, & Rolfs, 2017; Rolfs & Carrasco, 2012).

While the presence of the target after the saccade produced a fair amount of masking, it was the onset/offset signal of the distractor stimuli, rather than their presence, that produced the strongest reduction in performance. This suggests that two different processes contribute to intra-saccadic omission. First, the presence of the target after the saccade acts like a traditional backward mask, where the higher contrast input after the saccade disrupts further processing of the low contrast input during the saccade, reducing the phenomenal perception of the intra-saccadic stimulus. Second, the salient onset/offset signal of the distractor stimuli reduces phenomenal perception—either by withdrawing attention from the target stimulus, or by disrupting further processing of the target in an effect similar to backward masking (or both). **Experiment 2** sought to further examine the temporal properties of these two effects, and their combination, by more finely manipulating (1) the offset of distractor stimuli relative to the end of the saccade, and (2) the offset of the target stimulus relative to the end of the saccade. The effect of the most distant distractors, though small, had features that were most dissimilar from those expected from backward masking studies during fixation, thus we focused only on these distant distractors in **Experiment 2**.

4. Experiment 2

4.1. Materials and methods

4.1.1. Participants

Because we were examining what we expected to be a small effect, we recruited twice the number of observers as in **Experiment 1** (i.e., N = 20) through word of mouth and campus mailing lists. They were required to have normal or corrected-to-normal vision and gave informed consent prior to beginning the experiment. Monetary reimbursement was offered for their time (10 € for one session). Two participants did not complete enough experimental trials, and an additional three participants showed performance that did not rise above chance. We excluded these participants from further analysis, leaving 15 participants in the main analysis (further details below). The study was conducted in agreement with the latest version of the Declaration of Helsinki; it has been preregistered on the Open Science Framework (OSF; https://osf.io/4up6z/).

Apparatus and stimuli were the same as in **Experiment 1**.

4.1.2. Procedure

Procedure was the same as in **Experiment 1** with the following exceptions.

Instead of a practice block, we provided each participant with a short demonstration of the task and allowed them to perform a few trials to get used to making the correct eye movements. The experimenter would start data collection quickly after, to maximize the number of experimental trials that could be collected in one hour.

The trials had the same structure as in **Experiment 1**, except that we manipulated only one distractor condition: the offset timing of the 'far' distractor. Each trial began with the target and two distractors (9.5° above and below the target's initial position), and we removed the target and distractors at variable times relative to the expected completion of the saccade. We employed three separate manipulations: (1) we manipulated target duration after the saccade while the distractors disappeared upon saccade onset; (2) we removed the target before the end of the saccade and manipulated distractor timing; (3) the target remained on screen for long after the saccade (~310 ms) and we manipulated distractor timing. We chose six target offset timings (0, 10, 30, 70, 150, and 310 ms) and eight distractor offset timings (−40, −20, 0, 10, 30, 70, 150, and 310 ms) relative to the predicted end of the saccade. We based this timing on the average time to detect the saccade online (5 ms), and the average saccade duration (60 ms for a 16° saccade; Collewijn, Erkelens, & Steinman, 1988); with the target movement lasting 30 ms (and 8.33 ms from drawing the stimuli to the buffer until its presentation on the screen) this leaves 10 ms between the end of the target movement and the end of the saccade (with a 5 ms buffer). Thus, on trials where a stimulus was to be removed at 0 ms relative to the end of the saccade, the stimulus remained on screen for 10 ms after the target movement (approximately 45 ms from the beginning of the saccade); for trials where a stimulus was to be removed 10 ms after the end of the saccade, it remained on screen 20 ms after target movement, and so forth. There was some variability between the actual timing and the intended timing relative to the end of the saccade, resulting from variability in saccade durations and time to detect the saccade (Fig. 6, bottom).

All conditions were randomly interleaved and counterbalanced against saccade direction and stimulus movement direction, as in **Experiment 1**. We aimed to acquire 40 valid trials per condition and participant; with a total of 880 trials per participant to be completed over one session of approximately one hour. Two participants were unable to complete the full experiment within this time. One participant's saccades were consistently of too small amplitude; the other participant took too long entering responses. Their data were not included in the final analysis (as noted under *Participants*).

4.1.3. Analysis

Eye tracking: Eye tracking data was analysed as in **Experiment 1**.

Proportion correct: Following the removal of invalid trials, observers' proportion of correct responses was calculated in each condition (based on the intended timing) to examine differences in performance. An additional three participants were removed from the data pool at this stage as their performance did not rise above chance (as noted under *Participants*). Based on the initial calculation

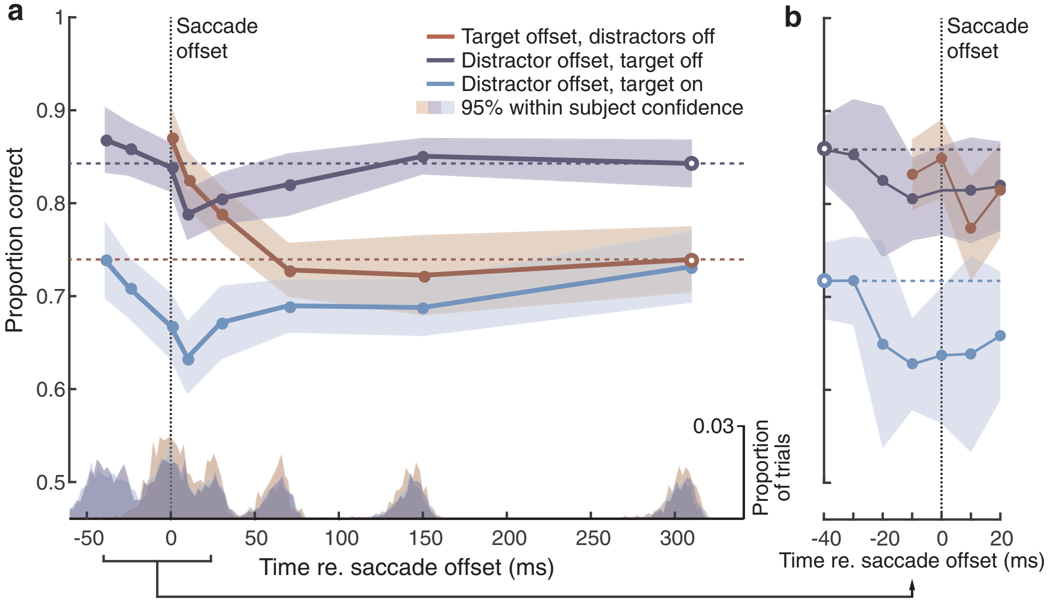

Fig. 6. Average proportion correct relative to intended target/distractor timing (a), and binned actual timing (b). (a) Proportion correct as a function of intended timings relative to saccade offset (vertical dashed line). Shaded areas correspond to 95% within-participant confidence intervals. The proportion of trials based on actual timing are shown along the base of the x-axis. (b) Proportion correct as a function of actual timings relative to saccade offset (vertical dashed line), in 10 ms bins. Horizontal lines provide references (cf. empty symbols), indicating performance when the target remains on long after saccade offset without distractors (red dashed line, based on the 310 ms target offset condition), and performance when the distractors remain on long after saccade offset, where the target is removed before saccade offset (dark blue dashed line, based on the 310 ms distractor offset, target off condition). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of proportion correct according to the intended timings, we further broke down performance based on the actual timing of the target/distractors relative to the end of the saccade around the key area from 40 ms before the end of the saccade to 30 ms after the end of the saccade.

4.2. Results

After the removal of two participants for not completing the task, and three for poor performance, we included the data of 15 participants in the analysis. We removed trials in which the saccade did not meet the required criteria (cf. **Experiment 1**), leaving an average of 37.7 (SD = 1.8) trials per timing condition, per participant. The average saccade duration was 65.2 ms (SD = 7.6), with the target stimulus movement starting on average 15.9 ms (SD = 3.2) after the start of the saccade and ending 19.7 ms (SD = 9.7) before the end of the saccade. The distributions of these timings were similar to those depicted in Fig. 2 for **Experiment 1**, though the time between the end of target movement and the end of the saccade was slightly longer, likely because of the longer saccade durations. The actual timings of the distractors and target were relatively narrowly distributed around the intended timings (Fig. 6a, bottom), though slightly earlier than intended (again, this was likely due to the slower saccades).

In the target-only conditions, performance was highest if the target disappeared by the end of the saccade, and dropped down significantly with increasing target duration after the saccade (Fig. 6a). In the distractor offset conditions, performance depended on the presence of the target after movement completion, averaging to ~85% correct in the target-off condition, and 70% correct in the target-on condition. Indeed, these two levels of performance are indistinguishable from performance in the 0 ms and 310 ms timings of the condition that did not feature distractors, respectively. Thus, overall, performance was dominated by the continued presence of the target stimulus after saccade landing.

However, we observed a sudden dip in performance if distractor offset occurred around the end of the saccade. For this reason, the exact time points between −40 and 30 ms from the end of the saccade were used to re-calculate performance based on bins of 10 ms (Fig. 6b). The reduction in the number of trials in these bins led to additional uncertainty in the performance estimates, as can be seen from the greater width in the confidence intervals, however, the dependence between performance and the timing of distractor offsets became more apparent. We observed a small drop in performance resulting from the offset of a distant distractor stimulus within the −20 to 20 ms window surrounding the end of the saccade, due to the additional variability, this performance drop is only significant in the [−1 0 0] ms time window, where the confidence intervals do not overlap with their baseline (dashed horizontal lines).

This closer investigation into the exact timings was not possible with the target offset timings beyond saccade offset, because of the larger gaps between intended timings. The pattern of performance based on the intended timings suggests that this is not necessary, as the effect of target timing on performance is realised over a longer time period, where the decrease in performance develops over the first 50 ms after the saccade is completed.

Thus, two distinct functions appear to describe the effects observed here—one representing the effect of the distant distractors and one representing the target masking itself. Performance was slightly but significantly reduced when the distant distractors offset around the time of the end of the saccade. This reduction in performance began prior to the end of the saccade in a steep drop that recovered at a slower rate, over 100–150 ms after the end of the saccade. In contrast, the persistence of the target after the saccade was accompanied by a far greater reduction in performance. The impairment relating to the persistence of the target stimulus developed over the first 50 ms after the saccade, where the effect saturated. These two distinct effects appeared to sum, as the pattern of reduced performance due to the distant distractors is seen in addition to the reduction associated with target persistence.

A control analysis of saccade amplitudes across all conditions showed that, as in **Experiment 1**, any difference in performance across conditions could not be explained by systematic differences in saccade amplitude: The mean amplitude across conditions was 17.82°, with a standard deviation of 1.44°. The range of average saccade amplitudes across conditions was 17.68–17.92°.

5. Discussion

We designed two experiments to explicate the spatial and temporal relationship of post-saccadic stimuli to reduced intra-saccadic perception. The first experiment tested the effect of the presence of distractor stimuli before, during and after the saccade in four locations (near the target stimulus, far from the target stimulus, inside the saccade path and outside the saccade path), and compared this with the effect of leaving the target stimulus on screen after the saccade ended. The results show that continued presence of the target stimulus after the saccade causes a reduction in participants' ability to report on the intra-saccadic stimulus; however, this was not sufficient to cause complete omission on every trial. In addition, the onset/offset signal of the distractor stimuli also reduced perception of intra-saccadic stimuli. This effect may be different from traditional backward masking during fixation (though this was not directly tested here), since even the offset of distant distractor stimuli reduced performance, and this effect did not depend on whether the distractor was within the path of the saccade or outside it.

We further explored this issue in Experiment 2, in which we finely assessed the impact of the timing of the target and distractor stimuli. We found two distinct functions that appeared to constitute separable influences on intra-saccadic perception. The strongest reduction in performance was caused by a sustained target stimulus after the saccade. The decline of performance builds with continued presence of the target over the first 50 ms after the saccade. On top of this, spatially distant transient signals in close temporal proximity to the end of the saccade cause a small but consistent drop in performance that appears most effective when the transient signal occurs in close temporal proximity to the end of the motion of the target stimulus—even if this occurs before the saccade has ended. These two effects have different temporal characteristics and appear to additively degrade task performance, suggesting they may be the result of two independent mechanisms both contributing to saccadic omission.

The effect of the target remaining on screen is temporally similar to what might be expected from the presentation of a mask during fixation. In our experiments, SOA was not manipulated; instead the stimulus remained on screen for a variable duration after the saccade. The decline in performance reaching a maximum when the stimulus remained on screen for 50 ms or more is essentially similar to fixational backward masking studies showing a decline in performance at very short SOAs when masks are of sufficiently long duration (Bachmann, 2015). One important difference between fixational masking studies and our experiment is that the mask stimulus does not completely spatially overlap with the motion streak it is masking. This may explain why masking was not complete in our experiments. Indeed, provided a complete visual scene is available at the end of an eye movement, regular backward masking as studied during fixation may provide sufficient explanation of the lack of awareness of the retinal input during a saccade.

The transient effect of the distant mask stimuli, however, follows neither the spatial nor the temporal properties of typical masking effects. These differences suggest that the omission of intra-saccadic stimuli may involve more than just backward masking. Interestingly, the effect of the transient signal on performance appears to begin before the end of the saccade. This suggests that these stimuli are being processed during the saccade (e.g., Watson & Krekelberg, 2009). This effect may therefore be better described by its temporal relation to the target motion (which is consistent within timing conditions plotted in Fig. 6a), as opposed to the time relative to the end of the saccade, although this assertion requires further investigation. The effect of these transient signals appears less dependent on the spatial relation to the target than has been shown in backward masking studies during fixation (Breitmeyer & Öğmen, 2006). It may, therefore, be better described as an attentional effect in which distractor stimuli draw resources away from visual processing of the target stimulus to a greater extent than they would if presented during fixation. Indeed, our target was not only the object of the perceptual task, it was also always displayed close to the movement goal. Before saccadic eye movements, visuospatial attention is rapidly allocated to the target of the saccade (Deubel, 2008; Rolfs & Carrasco, 2012) while other locations are processed to a much lesser extent (e.g., Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Montagnini & Castet, 2007; Ohl et al., 2017). To deal with the translation of the retina with respect to the world, these attended locations predictively remap to those locations on the retina that will contain the target upon saccade landing (here, the fovea; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). While attention can barely be divided from the target of a saccade before the movement starts (Deubel & Schneider, 1996; Kowler et al., 1995; Montagnini & Castet, 2007; Ohl et al., 2017), their remapped, post-saccadic counterparts may be vulnerable to distraction. The effectiveness of these transient signals at some distance from the target suggests that it is possible to distract spatial attention from the immediate onset of a post-saccadic fixation. Directly manipulating the effectiveness of attentional capture of the distractor stimuli in future experiments may shed further light on this effect.

It is interesting to note that participants—when debriefed after the experiments—described their phenomenal experience of the target stimulus as a vertical streak, suggesting they perceived its spatiotopic configuration during the saccade, despite it tracing a horizontally extended arc across the retina. This would suggest the influence of the onset/offset transients is not necessarily due to a lack of appropriate spatial localization of the distractor stimuli, particularly when they were onscreen during the saccade, and offset as the saccade ended. Perhaps the resources needed for creating a spatiotopic understanding of the intra-saccadic visual scene precludes strict spatial control of the selection of stimuli for privileged processing via attentional control. This would act to strengthen the effectiveness of saccadic backward masking relative to fixational backward masking, particularly if the spatial aspects of the scene are not optimal for masking across a saccade. This idea can be integrated into our understanding of stimulus localization around the time of a saccade and suggests that a ‘top-down’ form of stimulus location uncertainty may indirectly contribute to our everyday lack of awareness of the visual stimulation during a saccade.

Crucially, that onset and offset signals do have a negative impact on visual perception around the time of a saccade means that we might need to take more care in experimental design, as many studies of peri-saccadic perception manipulate the stimuli by having them appear or disappear. For example, in many displacement studies the target is offset and onset at a new location around the end of the saccade (Bridgeman, Hendry, & Stark, 1975). Deubel et al. (1996) showed that blanking the target stimulus for at least 50 ms after the end of the saccade improved observers’ ability to discriminate the direction of displacement. Our data suggest that the delay in the onset of the displaced target—and a resulting reduction in attentional distraction—may play a role in this improvement, beyond the impact of the absence of the target upon saccade landing.

The visual stimuli used in the present set of experiments are clearly quite different from those the average observer would experience on a daily basis. However, the presence of the target stimulus after the end of the saccade had a similar (although weaker) temporal effect as the naturalistic full field mask used in Campbell and Wurtz (1978). We therefore suggest that the results of our experiments should not be dismissed as unrealistic. In natural environments, where there is far more complex input both during and after the saccade, the small effects demonstrated here likely exist only in greater strength. Even the transient offset signal could be realised by changes in the natural environment, such as motion, or the occlusion of distant objects with changes in eye and head position. A further caveat is that the present study focuses to some extent on the omission of externally generated motion, orthogonal to the direction of eye movement (though the externally generated motion and motion caused by the eye movement are combined at the level of retinal input). It may be questioned whether the omission of externally generated motion differs mechanistically from the omission of motion signals generated by the eye movement itself.

The experiments presented in this paper have examined the effect of persistent and transient visual signals on saccadic omission (that is, the lack of phenomenal awareness of visual information around the time of a saccade), with an emphasis on how these effects relate to backward masking during fixation. Backward masking is just one of several factors that may influence an observer’s phenomenal awareness around the time of a saccade. Here, in addition to a backward masking effect we postulate is similar to passive fixational backward masking, we have found evidence that attentional mechanisms may also be an important factor in saccadic omission. The visual signals prior to the saccade also contribute to saccadic omission, by another form of masking, forward masking (Campbell & Wurtz, 1978). Another factor is saccadic suppression, which could explain the reduction in contrast sensitivity beginning ~50 ms before the onset of a saccade (Zuber & Stark, 1966), which specifically affects low spatial frequency stimuli defined by luminance (Burr, Holt, Johnstone, & Ross, 1982). The relative contribution of backward masking and saccadic suppression in creating saccadic omission is an interesting question, given that often these mechanisms are posed as competing hypotheses in the literature. In the experiments presented here, it is likely that saccadic suppression was reasonably constant across conditions (given there was no evidence for a difference in saccade amplitudes across conditions). However, as masking is more effective when the mask has higher ‘energy’ than the target (Breitmeyer & Öğmen, 2007), greater saccadic suppression would increase the effectiveness of backward masking (cf. Rolfs & Ohl, 2011). Conversely, as the reduction in contrast sensitivity begins before the onset of the saccade, the effectiveness of forward masking from the pre-saccadic input may be low by comparison. Finally, a recent model of saccadic suppression (Crevecoeur & Körding, 2017) suggests that suppression may increase with increasing noise in the peri-saccadic sensory information. In this situation, our onset and offset masking conditions would be expected to contribute additional noise to the intra-saccadic signals and thus increase the effectiveness of omission. Indeed, Zimmermann, Morrone, and Binda (2018) found some evidence of an increase in suppression in the first of two consecutive saccades when saccade targets are removed at the end of the first saccade. This suggests that investigating the relationship between post-saccadic (and pre-saccadic) visual input and saccadic suppression is an important avenue for future research.

6. Conclusion

In conclusion, we suggest that saccadic backward masking may be substantially realised by the same mechanism as fixational backward masking, where the sustained mask (> 50 ms) immediately after the saccade severely impairs intra-saccadic perception. It may, however, be enhanced by the greater power of distant transients to capture attention. According to the results of this study, we propose that our lack of awareness during a saccade may be best described by the combination of a passive masking mechanism and a reduction of top-down control of spatial attention.

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