Report

Backward Masking and Unmasking Across Saccadic Eye Movements

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Summary

Humans make several eye movements every second, and thus a fundamental challenge in conscious vision is to maintain continuity by matching object representations in constantly shifting retinal coordinates [1]. One possible mechanism for visual stability is the remapping of receptive fields around saccade onset, combining pre- and postsaccadic information [2]. The mislocalization of stimuli briefly flashed near the time of saccades [3–7] has been taken as evidence for remapping. Yet the relationship between remapping, mislocalization, and trans-saccadic integration remains unclear. We asked participants to identify a target stimulus presented around the time of saccade onset, which was immediately visually masked by a postsaccadic stimulus presented in the same spatial location (backward masking). Presenting two rapidly occurring events across separate fixations allowed us to investigate how the visual system reconstructs what happens during a saccade. We show that saccadic remapping resulted in perception of target and mask as either spatially segregated or integrated, depending on the exact timing of saccade onset. During segregation, the target was unmasked because it was perceived as displaced from the mask; during integration, the postsaccadic stimulus masked the presaccadic target (spatiotopic masking). Thus, segregation and integration may work together to yield continuity in conscious vision.

Results

To explore trans-saccadic vision, we adopted backward metacontrast masking, an experimental procedure in which the conscious perception of a briefly flashed stimulus (target) is reduced or eliminated by the subsequent occurrence in the same location of a larger stimulus (mask) that fits around the contours of the target without touching it [8]. Critically, targets were presented before or during a saccade, whereas the mask could appear after the saccade in the same spatial, but different retinal, position. Targets were either easily distinguishable from the masks (filled shapes) or identical to the masks but smaller in size (unfilled, or empty shapes). In the former condition, target and mask could be perceived as separate spatiotemporal objects: participants could see something before the mask, even though they could not say exactly what [9]. In the latter condition, in contrast, masking was generally

so complete that participants were entirely unaware that the target had been presented at all.

We presented targets near the onset of saccades in order to examine the time course of perisaccadic perception. Numerous studies have shown that neurons involved in visual-spatial representation change their receptive fields based on the anticipated outcome of the saccade, a phenomenon known as remapping [2]. The activity of these remapping neurons is not discretely tied to single fixations, but instead these neurons respond based upon information from the future, or even past, receptive field. If the remapping of receptive fields serves as a bridge for conscious perception, as we suggest, then this leads to the following predictions about the influence of saccades on backward masking: (1) when perisaccadic mislocalization occurs, the target should be unmasked and appear as segregated from the mask, thus increasing its visibility; and (2) when trans-saccadic integration occurs, the target should be hidden by the mask, even when the target and mask have different retinotopic coordinates.

Participants were cued to make saccades either to the left or to the right. Just before saccade onset, a target stimulus was briefly flashed and then, after a variable interstimulus interval (ISI), masked by a larger stimulus (the mask) shown at the same location. After the saccadic eye movement, participants reported the identity of the target (square or diamond) and where they perceived it compared to the mask (same location, to the left, or to the right; Figure 1).

Consistent with theories of remapping as an explanation for perisaccadic mislocalization [7], the proportion of displaced trials was greatest around the time of saccade onset (Figures 2A and 2B). When the target was shown more than 100 ms before the saccade, it was typically perceived in the correct location, whereas around the time of saccade onset, the target was displaced toward the saccade target on a majority of trials. The fact that mislocalization occurred so frequently might be considered surprising, given previous studies showing that the presence of a longer visual reference (in this case, the mask) can reduce mislocalization [10, 11]. Despite the presence of the visual reference, participants reported displacements of the target, particularly in the perisaccadic time period.

Moreover, the displacement perceptually unmasked the target (main effect of displacement across both filled- and empty-shapes conditions: F = 9.29, p = 0.016). In the filled-shapes condition (Figure 3A), displacement of the target in the direction of the saccade dramatically improved the ability to correctly report the target shape (F = 11.79, p = 0.009). This benefit of displacement was found even with the shortest ISI, in which only one blank frame of 12 ms separated target and mask (t = 2.75, p = 0.027). Participants were unable to correctly discriminate the target identity at the shortest ISI, for which d′ [12] was near zero (d′ = 0.84, standard deviation [SD] = 0.75) for filled shapes perceived veridically but equal to 1.9 (SD = 0.75) for displaced trials. As expected, accuracy generally increased for longer ISIs between target and mask (main effect of ISI: F = 39.56, p < 0.0001). Best performance in the strong-masking condition (ISI of 12 ms) was found near the time of the saccade (Figure 3C), consistent with

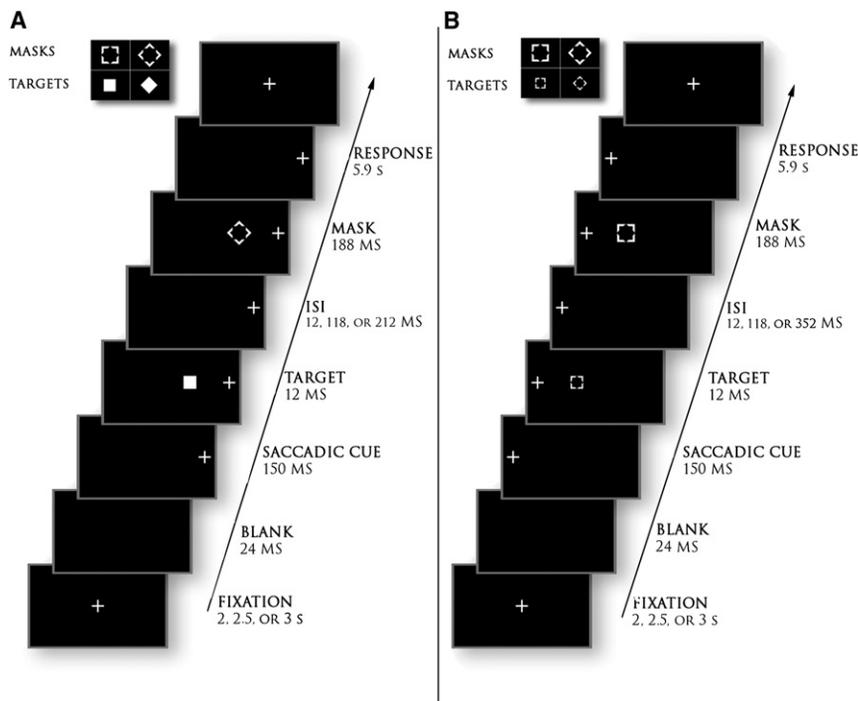*Correspondence: nicola.depisapia@unitn.it (N.D.P.), david.melcher@unitn.it (D.M.)

Figure 1. Experimental Design during Saccadic Blocks

Participants fixated a yellow central cross and then, after a variable blank delay, were presented with a lateral saccadic cue indicating the new fixation location. Prior to or during their actual eye movement, a target was briefly shown on the screen ipsilaterally to the requested saccade (white filled square or diamond in condition 1 [A]; white empty square or diamond for condition 2 [B]). After a variable interstimulus interval (ISI), a larger mask (white empty square or diamond) appeared in the same location as the target. We varied the ISI between the target and mask in order to directly manipulate the influence of the mask. The background was black throughout the experiment.

the hypothesis that displacement made the target more visible.

The empty-shapes condition allowed us to test the case in which the target and mask tended to be perceptually fused into a single object, showing stronger masking (main effect of filled versus empty shape: $F = 7.73$, $p = 0.024$). With these unfilled targets and no perceived target displacement, backward masking could completely eliminate any awareness of the presence of the target stimuli, especially at the shortest

ISI ($d' = 0.37$, SD = 0.41), with only gradual improvement with longer ISIs (Figure 3B). Performance was better on trials in which the target was perceived as displaced, compared to when the target was perceived at its actual location ($F = 5.55$, $p < 0.05$), even for the shortest ISI (mean $d' = 1.22$, SD = 1.5). As in the filled-shape condition, best performance was found in the perisaccadic time period (Figure 3D).

The empty-shape condition also provided the opportunity to test whether masking might continue even when the target and mask were separated by a saccadic eye movement. Previous studies have suggested that metacontrast masking occurs mainly in retinotopic coordinates [13]. When looking at trials in which the target was shown before the saccade and the mask shown after the saccade (Figure 4A), however, we found
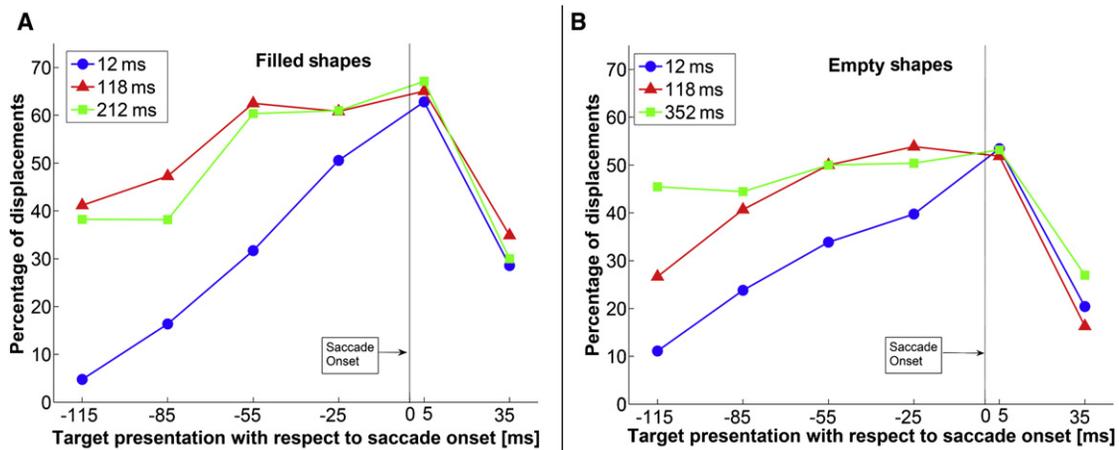

Figure 2. Percentage of Displacements as a Function of the Presentation Time of the Target with Respect to the Saccade Onset

In these panels, we report the percentage of perceived displacements for each ISI, respectively, for filled (A) and empty (B) shapes. Each data bin represents the average inside a 30 ms time period as a function of target presentation with respect to the initiation of the saccade. The data points are positioned at the center of the 30 ms interval. The vertical black line indicates the saccade onset time. The proportion of displacements varied across the bins ($F = 23.4$, $p < 0.0001$ for filled shapes; $F = 17.7$, $p < 0.0001$ for empty shapes). To further investigate the relationship between saccade onset and the perception of displacement, we performed multiple comparison tests. We used the −130 ms to −100 ms bin as baseline, because the targets appeared prior to the perisaccadic time period. There was a significant difference from the baseline for the bins ranging from −70 ms to 20 ms for the filled shapes and from −40 ms to 20 ms for the empty shapes, showing that perception of displacement is tightly related to the timing of the presentation of the target with respect to saccade initiation. There was a trend for displacements in the shortest ISI conditions to be more strictly constrained to the perisaccadic time period than with longer ISIs. For bins to the left of saccadic onset of −25 ms, the saccade onset was initiated after the disappearance of the target, thus suggesting that a remapping process accounts for the perception of displacement.
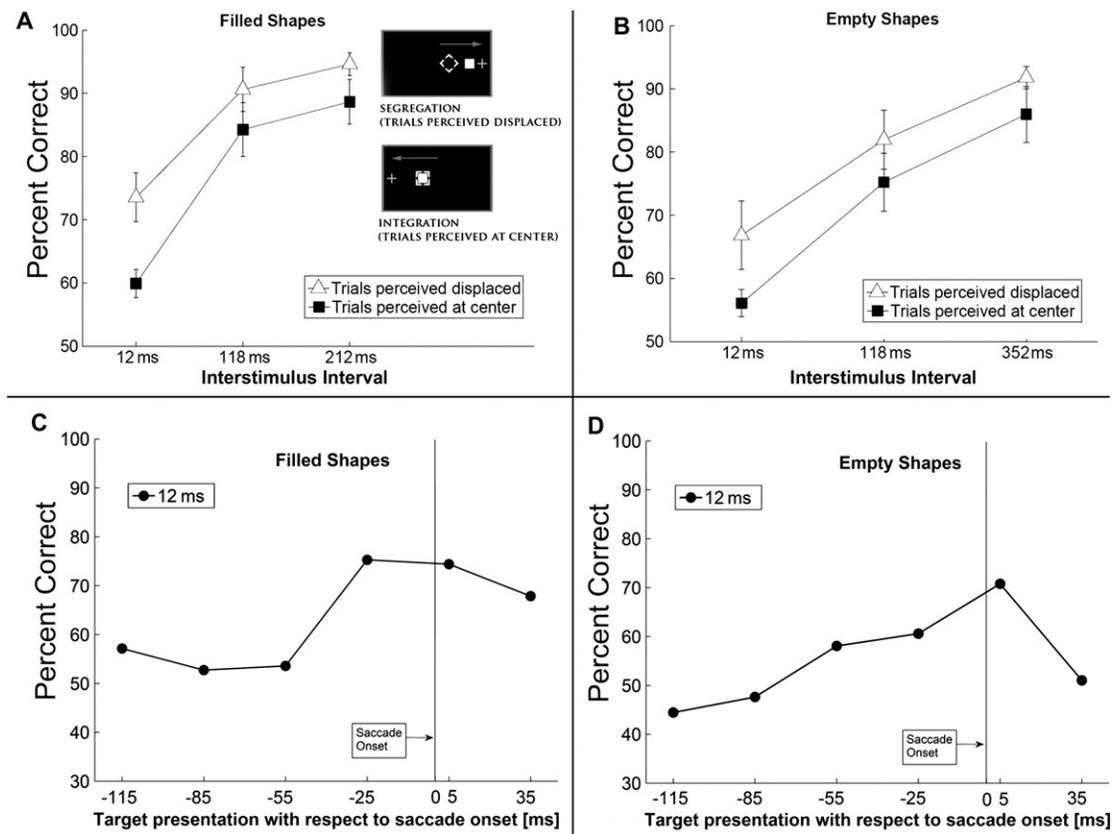
Figure 3. Target Discrimination Accuracy

The top row shows the percentage of trials in which the target shape was correctly reported as a function of ISI, whereas the second row shows performance in the shape discrimination task as a function of the timing of the target with respect to saccade onset (left panels for filled shapes, right panels for empty shapes).

(A and B) In the insets of panel A, we depict how participants subjectively perceived the target and mask locations in the filled-shape condition. The target and mask were always shown in the same spatial location on the screen, but the location of the target was not always perceived veridically. Observers reported seeing the target and mask in the same location when integrating (bottom inset) but in different locations when segregating (top inset). Notice how segregation increased the visibility of the target, even at the smallest ISI between target and mask. Error bars indicate standard error of the mean.

(C and D) Target detection accuracy as a function of target presentation with respect to saccade onset. Data is shown for trials with the shortest target/mask ISI (i.e., 12 ms). Accuracy for the other ISIs, where masking was weaker, remained relatively high (above 75%) and thus are not depicted.

evidence for trans-saccadic masking in spatial coordinates. First, performance was worse ($t = 2.75$, $p = 0.025$) when the mask was shown shortly after the saccade (ISI = 118 ms), compared to trials in which the mask was shown late in the trial (ISI = 352 ms) (Figure 4B). Overall, the postsaccadic mask had a greater influence when it was shown nearer in time to the target (main effect of postsaccadic ISI across filled and empty shapes: $F = 11.94$, $p = 0.009$). Second, there was a consistent trend for displacement to improve performance, even on trials in which the mask was shown postsaccadically (main effect of displacement across filled and empty shapes: $F = 6.22$, $p = 0.037$). Because the postsaccadic mask was shown at a different retinal location, we might have expected that performance on these trials would have been unaffected by ISI or displacement; instead, the main effects of displacement and ISI continued across the saccade.

To confirm that the decrement in performance on trials with the postsaccadic mask was due to masking rather than to a failure to see the target, we conducted a second experiment (see Supplemental Experimental Procedures available online) in which the strength of the masking was increased by reducing the blank interstimulus interval between the target and mask. If there was trans-saccadic masking, then we would predict strong masking when the mask and target locations were matched across the saccade, which is what we found (Figure 4C, left bar). In contrast, performance remained high when the mask location was vertically offset from the target (Figure 4C, right bar) ($t = 3.53$ $p < 0.05$). Thus, the inability to discriminate the target shape was neither due to the act of making a saccade nor to the mere presence of a postsaccadic stimulus. Instead, these results show that trans-saccadic masking can occur when the postsaccadic mask is shown in the same spatial coordinates as the target.

Discussion

Our main finding is that presaccadic targets were effectively unmasked by the saccade, even when the postsaccadic mask followed the target at the shortest ISI. This overall pattern of results is consistent with previous reports of peri-saccadic mislocalization of flashed targets but also shows that mislocalized stimuli can be perceived, in the case of masking, more accurately than their correctly localized counterparts. Thus, mislocalization in our task was likely related to saccadic remapping rather than to confusion or guessing about the target [14, 15]. Our results suggest that eye
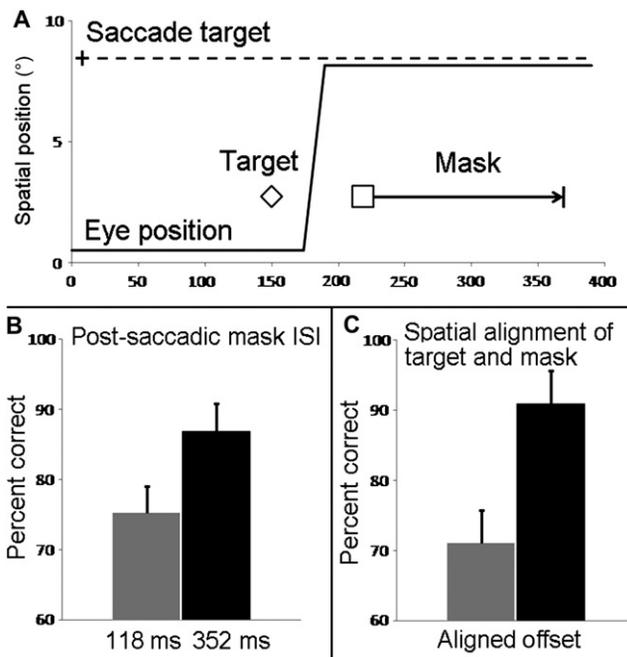
Figure 4. Trans-saccadic Masking in Spatiotopic Coordinates

(A) Trials were examined in which the saccade was made during the blank interval between the test and the mask stimulus. Note that this means that the target and mask were shown at different retinal positions (different visual hemifields) but at the same spatial location on the screen.

(B) In experiment 1, the masking continued across the saccade. Here, performance at discriminating the empty target shape for the two different postsaccadic ISIs of 118 ms (left bar) and 352 ms (right bar) is shown. The percentage correct on trials in which the mask was presented shortly after the saccade (ISI = 118 ms) was lower than on trials in which the mask was shown later in the trial (ISI = 352 ms), consistent with the predictions of trans-saccadic masking.

(C) Performance in experiment 2 (see Supplemental Experimental Procedures) in which the ISI was reduced to 48 ms in order to increase the strength of the masking. The mask was either shown in the same spatial location on the screen (left bar) or was slightly displaced vertically (right bar). Although performance with the spatially offset mask was near perfect, a consistent decrement in performance was found on trials in which the spatiotopic location of test and mask was matched across the saccade. Error bars in (B) and (C) indicate standard error of the mean.

movements increased the ability of the visual system to segregate target and mask as separate perceptual objects. Although saccades are often viewed as a problem for the visual system, our results suggest that the brain may take advantage of saccades to make perception more effective [16–18].

In addition, the strong masking found with unfilled targets led to trans-saccadic masking across the eye movement. This spatiotopic masking provides further evidence that the visual system interprets perceptual events as continuing across the saccade rather than beginning anew with each fixation [19–22]. Indeed, trans-saccadic integration can improve performance on some tasks [1, 23]. Previous studies have shown that when the identity or location of the stimulus is changed across the saccade, the presaccadic stimulus may be essentially overwritten by the postsaccadic one [24, 25], consistent with the idea of postsaccadic masking. Our results suggest that postsaccadic masking can also be interpreted in terms of integration of the pre- and postsaccadic information. When there is conflicting information about the object across

saccades, the visual system is likely to give preference to the more recent and thus more reliable postsaccadic information.

In addition, our findings have implications for theories about the circuits of consciousness. These results suggest that remapping can either route target information toward awareness when the target is identified as a unique object or hide the target from awareness when it is masked. Because remapping has been shown to be strongest in areas of posterior parietal cortex, where nearly 100% of neurons show remapping [26], our results support models in which visual awareness is mediated by recurrent signals from frontal-parietal to posterior visual areas [27–30]. Our results are consistent with the proposal that visual awareness of object location across saccades depends critically on the remapping of object pointers in sensorimotor location maps in parietal cortex [1, 7] that are part of the network of conscious perception.

Experimental Procedures

Two authors and seven naive observers took part in the study (five males, age range 22–38). All participants gave informed consent according to guidelines set by the University of Trento Ethical Committee. After running practice trials to familiarize themselves with the task, each participant completed two control blocks with no saccades (48 trials each; see Supplemental Experimental Procedures and Figures S1 and S3) and two saccade conditions (filled and unfilled shapes). Each saccade condition was made up of 8 blocks of 96 trials each. Examples of saccadic trials for each condition are illustrated in Figures 1A and 1B. In these trials, participants first fixated a yellow cross (0.7°) at the center of a black screen (80 cm viewing distance) for a variable period (2, 2.5, or 3 s). Fixation disappeared briefly (blank of 24 ms), and then a yellow cross (saccade cue) appeared at 8.3° left or right of center. After a brief delay (150 ms), a white target stimulus (size 0.7°; filled square or diamond for condition 1, unfilled square or diamond for condition 2) appeared ipsilaterally to the cue 2.8° to the left or right of the center for 11.7 ms. After a variable ISI (12, 118, or 212 ms for condition 1; 12, 118, or 352 ms for condition 2), the mask (size 1°; white unfilled square or diamond for both conditions) was presented for 188 ms on the same location as the target for the specific trial. The lateralized cross remained visible until participant's response or for a maximum of 5.9 s. Eye movements were recorded during each session (see Supplemental Experimental Procedures and Figure S2).

Participants pressed one of six buttons (on a keyboard) with their left or right hand to indicate target identity (mapped onto separate hands: left for diamonds and right for squares) and location (mapped onto three fingers of each hand: left, right, or same location of the mask).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at doi:10.1016/j.cub.2010.01.056.

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