



How post-saccadic target blanking affects the detection of stimulus displacements across saccades

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ABSTRACT

When a visual stimulus is displaced during a saccade the displacement is often not noticed unless it is large compared to the amplitude of the eye movement. Displacement detection is improved, however, if a blank intervenes between saccade target offset and the presentation of the displaced post-saccadic stimulus. This has been interpreted as evidence that precise information about eye position and accurate memory for the position of the pre-saccadic target are available immediately after saccade offset, but are overridden by the presence of the post-saccadic stimulus if it is present when the eyes land. In the current set of experiments we examined in more detail how blanking contributes to the increase in displacement sensitivity. In two experiments we showed that the presentation of a blank interval between saccade offset and the presentation of the displaced stimulus improved people's ability to detect that the stimulus had been displaced and also their ability to judge the direction that it had been displaced, but only for displacements opposite to the direction of the saccade (backward displacements). A third experiment suggested that this improvement in the detection of backward displacements was due in part to subjects misremembering the saccade target location as being closer to the initial fixation point than it actually was immediately after the saccade but remembering its location more veridically 50 ms later. This has the effect of improving the detection of displacements as well as their direction of displacement, but preferentially for backwards vs. forward displacements.

1. Introduction

Objects in the world appear to maintain their positions in space even though their positions on the retinas change with every eye movement. This has often been presumed to occur via an accurate compensatory mechanism that takes eye position into account in order to maintain visual stability of objects across eye movements (Bridgeman, van der Heijden, & Velichkovsky, 1994). Evidence against this hypothesis has been provided by the finding that displacing a visual stimulus during a saccadic eye movement is often not noticed. For example, Mack (1970) changed the position of a visual target by varying amounts during a subject's eye movement and found that target displacements greater than 10% of the saccadic movement were usually detected, but displacements under 10% were rarely detected. Whipple and Wallach (1978) reported effects of similar magnitude, and Bridgeman, Hendry, and Stark (1975) reported that participants often failed to detect stimulus displacements of 33% of saccade amplitude. This failure to detect "abnormal" retinal image movements during saccades suggests that any compensatory mechanism accompanying a saccade must be rather inaccurate.

More recently, however, Deubel and colleagues (Deubel, Bridgeman, & Schneider, 1998; Deubel & Schneider, 1994; Deubel, Schneider, & Bridgeman, 1996) found that the presentation of a blank (empty screen) for 50–300 ms in the period between saccade target offset and the presentation of the displaced post-saccadic stimulus improved substantially the detection of the direction in which the stimulus had been displaced. They interpreted this as evidence that precise information about eye position and a highly accurate memory for the position of the pre-saccadic target are always available after a saccade, but this information is not used if other visual information (i.e., the post-saccadic target stimulus) is present when the eyes land. That is, if the post-saccadic stimulus is visible immediately after the saccade (as it is under normal, no-blank conditions) then it appears to have been present continuously and the perceptual system assumes that it did not move unless the displacement is large (cf., MacKay, 1973; Matin et al., 1982). When the post-saccadic stimulus is not visible, however, then stimulus continuity is no longer assumed and precise information about eye position and highly accurate information about the position of the pre-saccadic target can be used to compensate for changes in the retinal position of the saccade target and improve detection of its

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displacement.

Using a procedure similar to that of Deubel and colleagues, Demeyer, De Graef, Wagemans, and Verfaillie (2010) and Tas, Moore, and Hollingworth (2012) also found that detection of the direction of stimulus displacement across a saccade was facilitated if a blank interval separated saccade onset and post-saccadic stimulus presentation. Using a different type of displacement judgment, however, Irwin and Robinson (2015) found that displacement detection per se was hurt by the presentation of a blank interval. In the Irwin and Robinson experiments participants had to report whether or not the saccade target was displaced at all, instead of having to report the direction in which it had moved. Irwin and Robinson found that detection was hurt by the presentation of a blank; in particular, blanking increased substantially the number of false alarms (i.e., participants reported that the saccade target had been displaced when in fact it had not). In sum, whereas several studies (e.g., Demeyer et al., 2010; Deubel et al., 1996, 1998; Tas et al., 2012) have shown that subjects are more accurate at detecting the direction in which a stimulus has been displaced when a blank interval separates saccade offset and stimulus onset, the results of Irwin and Robinson (2015) show that the presentation of a post-saccadic blank causes subjects to perceive stimulus displacement when in fact no displacement has occurred. This causes the false alarm rate to increase, thereby causing sensitivity to displacement to decrease in their experiments.

The results of Irwin and Robinson (2015) seem inconsistent with the notion that the pre-saccadic position of the saccade target is accurately stored in memory and that a precise eye position signal is available immediately after saccade onset but is overridden by the presence of the post-saccadic target stimulus. If such information were available, then it would seem that detection of stimulus displacements should also be improved rather than hurt by the presence of a blank interval because this information could be used to determine whether the stimulus had been displaced or not. The experiments that have found that blanking improves displacement detection have all used a task in which participants have to judge the direction in which a stimulus has been displaced, rather than whether a displacement has occurred at all, raising the possibility that blanking may improve the perception of motion direction rather than knowledge regarding the precise spatial position of a stimulus. For example, a small deviation in memory for the spatial position of the saccade target might be sufficient to trigger a displacement detection response when no displacement has actually occurred (causing a false alarm) while having little effect on judging the direction of motion. It is difficult to evaluate this, however, because the task used by Irwin and Robinson (2015) differed from that used by Deubel and others in several other ways in addition to the type of displacement judgment that was required. Thus, the purpose of the present study was to compare the effect of post-saccadic blanking on displacement direction performance (i.e., in which direction did the saccade target move) and displacement detection performance (i.e., did the saccade target move or not) in the same experimental paradigm.

2. Experiment 1

Two groups of subjects participated in Experiment 1 under blank and no-blank conditions. One group (the forward/backward group) judged in which direction a stimulus was displaced across a saccade, whereas the second group (the move/no-move group) judged whether a stimulus was displaced or not across a saccade.

2.1. Method

2.1.1. Participants

In total, 24 members (12 in each group) of the University of Illinois community participated in a single session that lasted approximately 50 min. They received \$6 for their participation. Participants reported that they had normal or corrected to normal vision and they were not

informed about the experimental hypotheses. All of the experiments reported in this paper were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The Institutional Review Board of the University of Illinois approved the research protocols. An informed consent form was signed by each participant before they took part in any experiment.

2.1.2. Stimuli and procedure

A 21-inch computer monitor (ViewSonic G810 CRT) was used for stimulus presentation. The refresh rate was 85 Hz. An Eyelink II video-based eyetracker (SR Research Ltd., Mississauga, Ontario, Canada) was used to record eye position. This system has a temporal resolution of 500 Hz, a spatial resolution of 0.1°, and a pupil-size resolution of 0.1% of pupil diameter. The participants sat with their heads in a chinrest 49 cm from the display. The stimuli were black and were presented on a white background (luminance = 86.3 cd/m²). A Microsoft Sidewinder digital game controller connected to the eye-tracking computer collected participants' manual responses.

The eye tracker was calibrated before each block of experimental trials by having participants fixate the edges and center of the display monitor. The sequence of events on each trial was based on that used in Experiment 2 of Deubel et al. (1996). Participants fixated a drift correction dot subtending 0.6° at the beginning of each trial and pressed a button on the game controller to initiate each trial. A blank screen was then presented for 506 ms, followed by the presentation of a cross (subtending 0.8° by 0.8°) at the display's center. A 506 ms delay ensued before this cross was erased and another cross (subtending 0.8° by 0.8°) was presented to the left or to the right, either 6° or 8° away. Subjects made a saccade to this peripheral cross, which was removed from the display upon detection of saccade onset. The cross was then presented again, either during the saccade (no-blank condition) so that the cross was present on the screen when the saccade ended, or following a 300 ms delay (blank condition), long after the saccade had ended and while the subject was fixating the blank screen. This cross was displaced with respect to its original position (or not) by some amount (−2°, −1°, 0°, 1°, or 2°), where negative displacements denote backwards displacements (i.e., in the opposite direction from the saccade), positive displacements denote forward displacements (i.e., in the same direction as the saccade), and 0 represents no displacement. One group of subjects (the forward/backward group) judged whether the cross had been displaced in a forward or backward direction, whereas a second group of subjects (the move/no-move group) judged whether the cross had been presented in its original position or in a new, displaced, position. Participants made their responses by pressing buttons (arrayed vertically) on the game controller. Participants received no feedback regarding the accuracy of their responses.

Each participant completed 520 trials. Saccade direction (left vs. right), saccade distance (6° or 8°), displacement distance (−2°, −1°, 0°, 1°, or 2), and blank condition (0 or 300 ms blank) were counter-balanced but across trials the conditions appeared in a random sequence. Participants received a break and were recalibrated after every 52 trials.

2.2. Results

Trials were not included in the analyses if the experiment program failed to detect a saccade, if the display change was not completed during the saccade, or if the participant failed to follow instructions. Table 1 presents information about saccade latencies, amplitudes, and durations as a function of saccade distance and saccade direction for both groups of subjects. Saccade distance and saccade direction were varied solely to create uncertainty about the initial position of the saccade target and were not considered further in the remaining analyses. The results for the forward/backward group will be discussed first, followed by the results for the move/no-move group.

Table 1

Mean latency, duration, and amplitude of saccades as a function of saccade direction and saccade distance in experiment 1 (standard errors in parentheses).

		Latency 6°	Duration 6°	Amplitude 6°	Latency 8°	Duration 8°	Amplitude 8°
Forward/Backward	Left	235 (15.2)	37 (0.9)	5.9 (0.16)	239 (15.9)	43 (1.1)	7.7 (0.15)
	Right	204 (12.8)	38 (1.1)	5.5 (0.13)	211 (12.7)	42 (1.5)	7.2 (0.19)
Move/No-Move	Left	222 (14.7)	39 (1.0)	5.5 (0.21)	227 (24.0)	43 (0.8)	7.2 (0.28)
	Right	203 (5.8)	39 (0.9)	5.4 (0.19)	202 (11.8)	44 (0.8)	7.2 (0.21)

2.2.1. Forward/backward results

Sensitivity to stimulus displacement is dependent on saccade amplitude, so trials in which the saccade amplitude was less than 2° (3.5% of trials) or was greater than 10° (2.2% of trials) were not included in the analyses. Also excluded were trials in which the initial saccade was made in the wrong direction (2.4% of trials), the display change did not take place during the saccade (11.4% of trials), or participants failed to report in which direction the saccade target had been displaced (0.7% of trials). After these exclusions, 79.8% of the trials remained for analysis.

The proportion of “forward” responses for no-blank (left panel) and blank (right panel) trials as a function of displacement distance is shown in Fig. 1 for each subject. The results are very similar to those reported by Deubel et al. (1996). On no-blank trials the psychometric functions were broad, indicating little sensitivity to the direction of displacement, and there was considerable inter-subject variability. Most subjects also exhibited a bias to respond “forward”, in some cases even for backwards displacements of 2°. In contrast, on blank trials the psychometric functions were considerably steeper, indicating greater sensitivity to the direction of displacement. There was also less inter-subject variability, and most subjects were relatively unbiased.

To quantify these results, cumulative Gaussian functions were fit to the data of each subject, and the means (points of subjective equality between “forward” and “backward” judgments, a measure of bias) and standard deviations are plotted in Fig. 2 for no-blank and blank trials (cf. Fig. 9 of Deubel et al., 1996). The fits of the cumulative Gaussian functions were quite good ($r^2 > 0.9$) for 9 of the 12 subjects but were less good for 3 subjects in the no-blank condition (subject 2, $r^2 = 0.83$; subject 7, $r^2 = 0.17$; subject 11, $r^2 = 0.76$; the fit for subject 7 was also poor in the blank condition, $r^2 = 0.84$). Paired t-tests on the data including all of the subjects confirmed that subjects were more biased to

respond “forward” on no-blank trials (mean = -2.6°) than on blank trials (mean = 0.04°), $t(11) = 3.0$, $sd = 3.05$, $p < .02$, and responses were more variable on no-blank trials (mean = 2.07) than on blank trials (mean = 0.87), $t(11) = 2.27$, $sd = 1.83$, $p < .05$. Paired t-tests excluding subjects 2, 7, and 11 yielded similar results; subjects were more biased to respond “forward” on no-blank trials (mean = -1.46°) than on blank trials (mean = 0.12°), $t(8) = 4.35$, $sd = 1.09$, $p < .005$, and the difference in variability between no-blank (mean = 1.17) and blank (mean = 0.71) trials was marginally significant, $t(8) = 1.69$, $sd = 0.83$, $p < .07$.

The change in subjects’ bias to respond “forward” on blank vs. no-blank trials was not due to differences in the position of the eyes during the time of post-saccadic stimulus presentation. On no-blank trials the eyes were located .09° short of the initial saccade target location while the post-saccadic stimulus was presented and on blank trials they were located .08° short of the initial saccade target location while the post-saccadic stimulus was presented. This difference was not significant, $t(11) = 0.13$, $sd = .16^\circ$, $p > 0.8$.

2.2.2. Move/no-move results

Trials were not included in the analysis if the initial saccade went in the wrong direction (2.4% of trials), if the saccade amplitude was less than 2° (4.0% of trials) or was greater than 10° (2.7% of trials), if the display change was not completed before the saccade ended (12.4% of trials), or if subjects failed to report whether the stimulus had been displaced or not (0.9% of trials). Following these exclusions, 76.4% of the trials remained for analysis.

The proportion of “move” responses for no-blank and blank trials as a function of displacement distance is shown in Fig. 3, averaged across subjects.

Inspection of Fig. 3 indicates that participants were more likely to

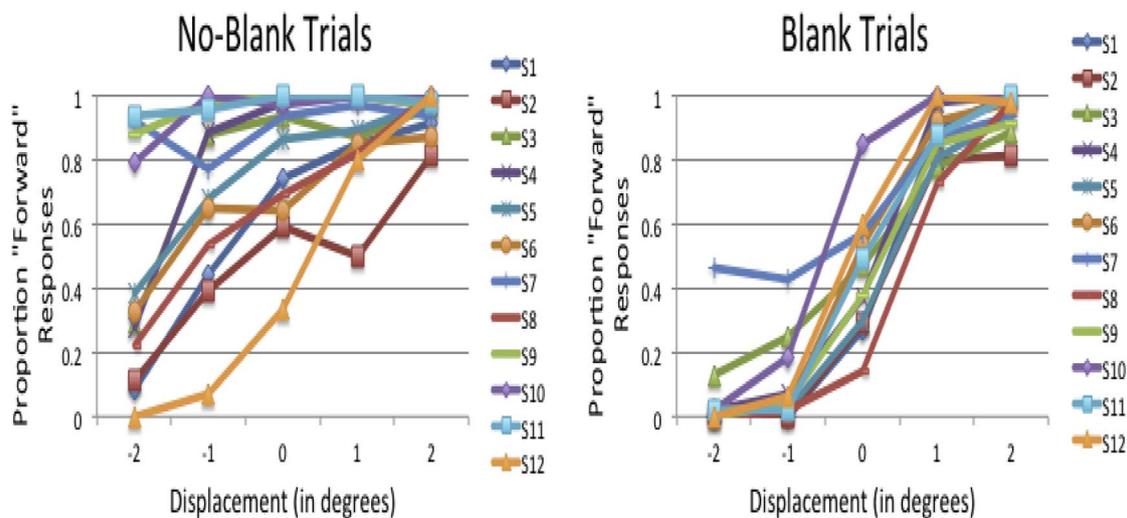


Fig. 1. Proportion of displacements judged to be in the forward direction (the same direction as the saccade) as a function of displacement size on no-blank and blank trials for each participant in Experiment 1. Negative displacements denote target jumps in the direction opposite the saccade.

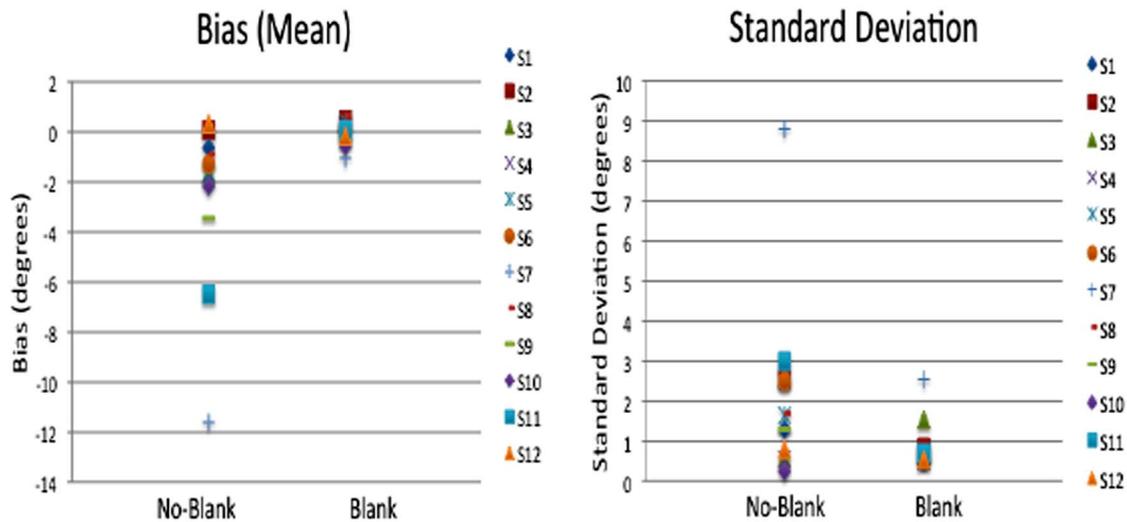


Fig. 2. Means (points of subjective equality between “forward” and “backward” judgments) and standard deviations for no-blank and blank trials for each participant in Experiment 1.

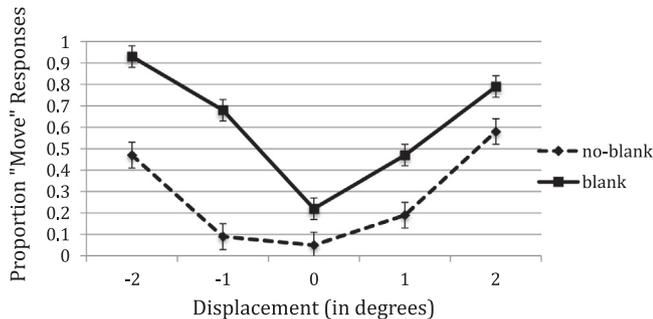


Fig. 3. The proportion of “move” responses for no-blank and blank trials as a function of displacement distance averaged across subjects in Experiment 1. Error bars depict standard errors.

report that they perceived a stimulus displacement across the saccade on blank than on no-blank trials. This was especially true for backwards displacements. Note that “move” responses on 0° displacement trials constitute false alarms, because the stimulus did not move on these trials. The false alarm rate was much higher on blank trials (0.23) than on no-blank trials (0.05), as in Irwin and Robinson (2015), who reported false alarm rates of 0.23 and 0.07 on blank and no-blank trials respectively on trials in which the saccade target was probed. A two-way repeated-measures ANOVA was conducted on the “move” responses with factors of blank condition (no-blank vs. blank) and displacement (−2°, −1°, 0°, 1°, 2°). The proportion of “move” responses was higher on blank (0.62) than on no-blank (0.27) trials, $F(1, 11) = 59.2$, $p < .001$, $MSe = 0.059$. There was also a main effect of displacement, $F(4, 44) = 34.9$, $p < .001$, $MSe = 0.041$. The interaction between blank condition and displacement was also significant, $F(4, 44) = 12.4$, $p < .001$, $MSe = 0.014$. Inspection of Fig. 3 suggests that blanking had a larger effect on backwards than on forward displacements, and it appears that the increase for forward displacements was no larger than the increase in the false alarm rate (i.e., the increase (0.18) when the displacement was 0°). To assess this, the error term from the interaction was used to construct a 95% Scheffe confidence interval, which is a conservative test for making multiple protected comparisons (Winer, 1971), to test whether the effect of blanking at the forward and backward displacements was significantly larger than the increase of 0.18 in the false alarm rate. The size of this confidence interval (interaction contrast) was ± 0.22 , so the effect of blanking at other displacements would have to exceed 0.40 (i.e., $0.18 + 0.22$) to be significantly greater than the increase in the false alarm rate caused by

blanking. Based on this we can conclude that blanking significantly increased the proportion of “move” responses over and above the increase in the false alarm rate for backward displacements of −1° (0.58) and −2° (0.46), but the increase for forward displacements of 1° (0.29) and 2° (0.21) were not significant.

2.3. Discussion

The results of the forward/backward group replicated those of Deubel and colleagues very closely. On no-blank trials most subjects showed little sensitivity to the direction of displacement and most exhibited a bias to respond “forward”, in some cases even for backwards displacements of 2°. This was true in the Deubel et al. (1996) study as well. In contrast, on blank trials most subjects were relatively unbiased and showed greater sensitivity to the direction of displacement. In other words, blanking improved performance when subjects had to judge the direction in which a stimulus was displaced during a saccade, as Deubel and others have found (e.g., Demeyer et al., 2010; Deubel et al., 1996, 1998; Tas et al., 2012).

The results for the move/no-move group showed that blanking increased the false alarm rate, as Irwin and Robinson (2015) found. Blanking improved performance when the stimulus was displaced, however, but only for the detection of backwards displacements and not forward displacements. This is somewhat contrary to the findings of Irwin and Robinson (2015), who found that blanking hurt overall displacement detection. The procedure used in the current experiment differed in several ways from that used by Irwin and Robinson (2015), however, so some aspect of the Irwin and Robinson (2015) procedure would appear to account for their finding that blanking hurt displacement detection across saccades. Possible reasons for this are discussed in the Section 5.

The finding from the move/no-move group that blanking improved performance only for the detection of backwards displacements and not forward displacements appears to be reflected in the results of the forward/backward group as well, in that blanking appears to improve subjects’ discriminability of backwards displacements, thereby reducing their tendency to respond “forward” on backward displacement trials. Thus, the results of the move/no-move group and the forward/backward group appear to be consistent in showing that blanking improves specifically the detection of backward displacements and not all displacements per se.

Why might this be? One possible explanation is suggested by studies that have shown that a visual stimulus presented briefly just before saccade onset or during a saccade is systematically misperceived in the

direction of the saccade target but becomes more veridical after the eyes have landed (e.g., Honda, 1993; Mateeff, 1978; Matin & Pearce, 1965; Ross, Morrone, & Burr, 1997). In the context of the present experiment, the effect of this might be to cause the post-saccadic stimulus to be perceived in a more forward direction under no-blank conditions, but more accurately under blank conditions, thereby producing the pattern of results that we observed. We think this explanation is unlikely for two reasons. One is that the post-saccadic stimulus in our experiment and in the Deubel et al. (1996) experiments was not presented briefly, but rather remained on the screen until the subject responded, so it is not clear if the same misperception would occur as for a briefly-presented stimulus. Zimmermann, Morrone, and Burr (2013) found that information about the spatial position of the saccade target improved as exposure duration increased, so the same may be true for a post-saccadic stimulus as well. Secondly, mislocalizations solely in the direction of the saccade have only been found in total darkness; under higher illumination conditions symmetric compression toward the saccade target is found (e.g., Ross et al., 1997), whereas we found an asymmetry between forward and backward displacements.

Thus, we propose instead that subjects misremember the position of the saccade target (rather than the post-saccadic stimulus) immediately after saccade onset but have a more accurate representation of its position when a blank interval intervenes before the post-saccadic stimulus is presented. The results for both groups of subjects are consistent with the hypothesis that the saccade target is misremembered as being closer to the fixation point immediately after the saccade, which would have the effect of making backwards displacements harder to detect and forward displacements easier to detect across the saccade.

Although this hypothesis may account for some of our results, it does not explain why the pattern reverses on blank trials—that is, instead of becoming symmetric, the proportion of “move” responses was actually considerably higher for backward displacements than for forward displacements on blank trials. Similar results were found by Irwin and Robinson (2014, 2015), who hypothesized that detection of backward displacements was facilitated because the initial saccade to the saccade target typically undershoots the target (as it did in this experiment) and thus a backwardly-displaced post-saccadic stimulus is presented closer to the fovea and benefits from being encoded with greater spatial resolution. Another possibility is that a backward displacement may result in the post-saccadic stimulus being presented in the opposite visual field from the original saccade target; for example, if a saccade is made to the right and the post-saccadic stimulus is displaced backward (to the left), it may be presented in the left visual field instead of the right and might be more easily noticed than if the post-saccadic stimulus is displaced forward such that it is presented in the same visual field (right) as the saccade target. This hypothesis was supported by a post hoc analysis that showed that under blank conditions, displacements that appeared in the opposite visual field from the saccade target were detected more often than those that appeared in the same visual field as the saccade target (69% vs. 57%, respectively, $t(11) = 2.43$, $sd = 0.17$, $p < .03$). This pattern was reversed on no-blank trials (28% vs. 31%, respectively) but was not significant, $t(11) = 0.45$, $sd = 0.23$, $p > .65$, presumably because the perceptual

system assumes stability under no-blank conditions and is thus insensitive to this cue.

The purpose of Experiment 2 was to obtain additional information about the time course of the blanking effect by investigating the effect of multiple blank durations on performance. This was explored by Deubel et al. (1996) and they found that accuracy for forward/backward judgments increased rapidly as blank duration increased from 0 to 100 ms. In Experiment 2 we compared the effect of increasing blank duration in the forward/backward task and the move/no-move task.

3. Experiment 2

As in Experiment 1, two groups of subjects participated, a forward/backward group and a move/no-move group. Across trials, displacement distances of -1° , 0° , and 1° were used, while blank durations of 0, 50, 100, 180, and 300 ms were used. Another difference from Experiment 1 is that an equal number of move and no-move trials were used in Experiment 2. In the first experiment the saccade target moved on 80% of the trials and did not move on 20% of the trials; this might have biased subjects to respond “move” on a high proportion of trials, thereby increasing the false alarm rate. To eliminate this possibility, for both groups of subjects in Experiment 2 the 0° displacement occurred on 50% of the trials, and displacements of -1° and 1° each occurred on 25% of the trials.

3.1. Method

3.1.1. Participants

As in the first experiment, 24 members (12 in each group) of the University of Illinois community participated in a single session of approximately 50 min in duration. They received \$6 for their participation. Participants reported that they had normal or corrected to normal vision and they were not informed about the experimental hypotheses. None had taken part in the first experiment.

3.1.2. Stimuli and procedure

The same apparatus was used as in the first experiment. The procedure was the same as in Experiment 1, except that the post-saccadic stimulus was presented after a delay of either 0, 50, 100, 180, or 300 ms. Each participant completed 560 trials. Saccade direction (left vs. right), saccade distance (6° or 8°), displacement direction (-1° , 0° , or 1° ; recall that there were twice as many 0° displacements as -1° or 1° displacements), and blank duration (0, 50, 100, 180, 300 ms) were counterbalanced but across trials the conditions appeared in a random sequence. Participants received a break and were recalibrated after every 80 trials.

3.2. Results

Trials were not included in the analyses if the experiment program failed to detect a saccade, if the display change was not completed during the saccade, or if the participant failed to follow instructions. Table 2 presents information about saccade latencies, amplitudes, and

Table 2

Mean latency, duration, and amplitude of saccades as a function of saccade direction and saccade distance in experiment 2 (standard errors in parentheses).

		Latency 6°	Duration 6°	Amplitude 6°	Latency 8°	Duration 8°	Amplitude 8°
Forward/Backward	Left	248 (39.1)	33 (1.6)	6.2 (0.27)	211 (27.7)	37 (1.0)	7.9 (0.27)
	Right	206 (32.2)	33 (1.3)	5.9 (0.19)	209 (30.1)	36 (1.6)	7.6 (0.24)
Move/No-Move	Left	196 (12.5)	38 (0.8)	6.0 (0.11)	199 (13.1)	43 (1.3)	7.8 (0.14)
	Right	193 (20.2)	39 (1.5)	6.1 (0.08)	195 (15.6)	43 (1.5)	7.8 (0.12)

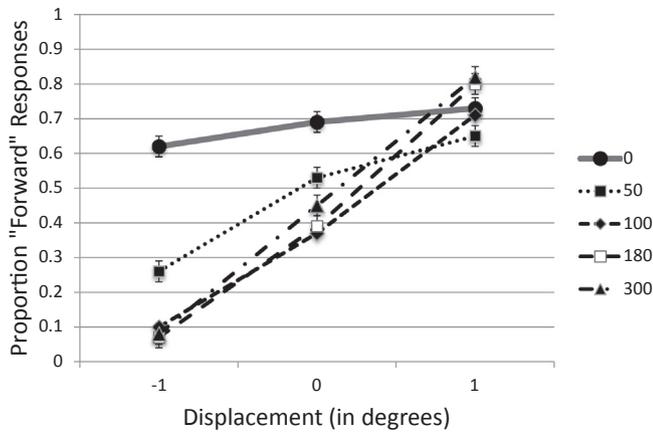


Fig. 4. The proportion of “forward” responses as a function of displacement direction for blank durations of 0–300 ms in Experiment 2, averaged across subjects. Error bars depict standard errors.

durations as a function of saccade distance and saccade direction for both groups of subjects.

3.2.1. Forward/backward results

As in Experiment 1, trials in which the saccade amplitude was less than 2° (6.8% of trials) or was greater than 10° (4.9% of trials) were not included in the analyses. Also excluded were trials in which the initial saccade was made in the wrong direction (2.6% of trials), the display change did not take place during the saccade (4.6% of trials), or participants failed to report in which direction the saccade target had been displaced (1.9% of trials). After these exclusions, 79.3% of the trials remained for analysis.

Fig. 4 shows the results, presenting the proportion of “forward” responses as a function of displacement direction for blank durations of 0, 50, 100, 180, and 300 ms. As in Experiment 1, this figure suggests that the improvement in accuracy as blank duration increased was largely due to improvements in detecting backward displacements. Participants were biased to respond “forward” to all displacements when there was no blank, replicating Experiment 1; as blank duration increased, “forward” responses to backward displacements declined rapidly, “forward” responses on no displacement trials declined as well to approximately 50%, and “forward” responses to forward displacements increased only slightly as blank duration increased. These trends were examined statistically in a repeated measures ANOVA with factors of displacement direction (backward, no, forward) and blank duration (0, 50, 100, 180, 300 ms). The main effect of displacement direction was significant, $F(2, 22) = 83.6$, $p < .001$, $MSe = 0.05$, as was the main effect of blank duration, $F(4, 44) = 12.7$, $p < .001$, $MSe = 0.04$. The interaction was also significant, $F(8, 88) = 26.6$, $p < .001$, $MSe = .0088$. The error term for this interaction was used to construct a 95% Scheffe confidence interval; the size of this confidence interval was .155 for pairwise comparisons. Thus, there was a significant difference in the proportion of “forward” responses on forward displacement trials between the 50 ms (0.65) and 300 ms (0.82) blank durations and significant decreases in “forward” responses from 0 to 50 ms and from 50 to 100 ms on both no displacement (0.69, 0.53, 0.37) and backward displacement (0.62, 0.26, 0.10) trials. No other pairwise comparisons were significant.

3.2.2. Move/no-move results

As in Experiment 1, trials in which the saccade amplitude was less than 2° (5.6% of trials) or was greater than 10° (5.2% of trials) were not included in the analyses. Also excluded were trials in which the initial saccade was made in the wrong direction (2.2% of trials), the display change did not take place during the saccade (3.7% of trials), or participants failed to report in which direction the saccade target had been

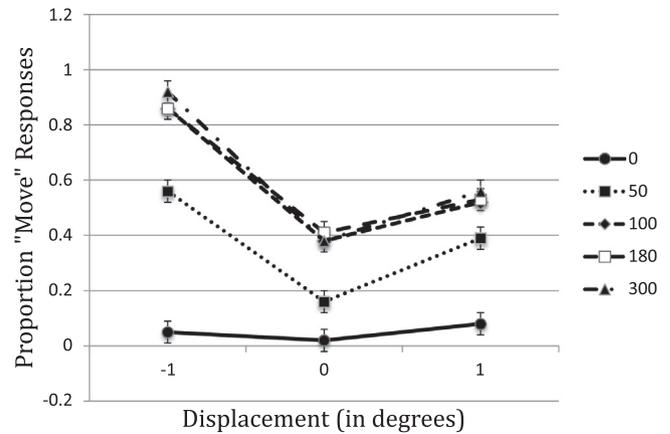


Fig. 5. The proportion of “move” responses as a function of displacement direction for blank durations of 0–300 ms in Experiment 2, averaged across subjects. Error bars depict standard errors.

displaced (0.7% of trials). After these exclusions, 82.7% of the trials remained for analysis.

The proportion of “move” responses as a function of displacement direction for blank durations of 0–300 ms, averaged across subjects, is shown in Fig. 5. The results replicate those of Experiment 1 in showing that there are few “move” responses under no-blank (0 ms duration) conditions but a high proportion under blank conditions, increasing to asymptote at a blank duration of 100 ms. This was true even though, unlike in Experiment 1, the number of “move” and “no-move” trials was equated in this experiment. The false alarm rate was higher here than in Experiment 1, perhaps because smaller displacements were used (-1° to 1° rather than -2° to 2°), making it more difficult to discriminate “move” from “no-move” trials. Importantly, as in Experiment 1, the effect of blanking was much higher on backward displacement trials than on forward displacement trials. An ANOVA showed that the main effect of displacement direction was significant, $F(2, 22) = 32.8$, $p < .001$, $MSe = 0.064$, as was the main effect of blank duration, $F(4, 44) = 82.7$, $p < .001$, $MSe = 0.023$. The interaction was also significant, $F(8, 88) = 14.0$, $p < .001$, $MSe = .009$, reflecting the fact that the proportion of “move” responses was not affected by displacement type when the blank duration was 0 but increased at different rates and reached asymptote at different levels as blank duration increased.

3.3. Discussion

The results of the forward/backward group replicated those of Deubel et al. (1996) by showing that accuracy at detecting the direction of displacement increased as blank duration increased. In addition, however, they showed that the improvement was due largely to improvements in detecting backward displacements. This mirrors the results of Experiment 1, which also found that the beneficial effects of blanking were largely exhibited on backward displacement trials.

The results for the move/no-move group are consistent with those of the forward/backward group in showing that blanking helps the detection of backward displacements but not forward displacements, as in Experiment 1. In addition, as in Experiment 1 the proportion of “move” responses was slightly higher for forward displacements than for backward displacements on no-blank trials (0 ms blank duration) but this pattern reversed for blank durations of 50 ms and longer.

The results for both groups of subjects are consistent with the hypothesis that the target is misremembered as being closer to the fixation point immediately after the saccade, thereby making backwards displacements harder to detect and forward displacements easier to detect across the saccade. It appears that over a period of 50–100 ms more accurate information about the position of the saccade target becomes

available in memory, perhaps because more accurate information about eye position becomes available, as hypothesized by Deubel and colleagues. The effect of this is to improve participant's ability to make forward/backward judgments. This information appears not to be completely accurate, however, because participants still make a considerable number of false alarms when a move/no-move judgment has to be made; the detection of both forward and backward displacements also increases as blank duration increases, however, with better detection of backward displacements presumably for the reasons discussed in Experiment 1.

The hypothesis that participants misremember the position of the saccade target immediately after saccade onset but have a more accurate representation of its position a short time later was investigated directly in Experiment 3 by explicitly probing subjects' memory for the position of the saccade target at various intervals after the saccade.

4. Experiment 3

4.1. Method

4.1.1. Participants

Twelve members of the University of Illinois community participated in a single session of approximately 50 min in duration. They received \$6 for their participation. Participants reported normal or corrected to normal vision and they were not informed about the experimental hypotheses. None had taken part in either of the first two experiments.

4.1.2. Stimuli and procedure

The apparatus was the same as in the first two experiments. The sequence of events on each trial was similar to that employed in Experiment 2 except that the post-saccadic stimulus consisted of a ruler (2° high) that subtended the entire width of the display (cf., Mateeff, 1978; Ross et al., 1997). The ruler is depicted in Fig. 6; the spaces between the markings on the ruler were .25°.

Subjects used the computer mouse to click on the ruler at where they thought the center of the saccade target had been presented. The ruler remained present on the display until they made their response. No feedback was provided.

Each subject completed 560 trials. Saccade direction (left vs. right), saccade distance (6° or 8°), and blank duration (0, 50, 100, 180, 300 ms) were counterbalanced but across trials the conditions appeared in a random sequence. Participants received a break and were recalibrated after every 80 trials.

4.2. Results

Trials were not included in the analysis if the initial saccade was made in the wrong direction (3.1% of trials), if the amplitude of the saccade was less than 2° (6.2% of trials) or was greater than 10° (3.6% of trials), or if the saccade ended before the display change was completed (3.1% of trials). On 0.7% of trials the computer software failed to output the mouse click so those trials were excluded as well. After these exclusions, 86.4% of the trials remained for analysis. Table 3 presents information about saccade latencies, amplitudes, and durations as a function of saccade distance and saccade direction.

Fig. 7 displays the mean mouse click position relative to the center of the saccade target as a function of blank duration. Negative values signify that the mean mouse click position underestimated the actual saccade target position (i.e., was between the saccade target location

and the central fixation point). A one-way ANOVA with blank duration as the sole factor was significant, $F(4, 44) = 6.7$, $p < .0001$, $MSe = 0.011$; the size of a 95% Scheffe confidence interval for this effect was 0.14°, so the mean mouse click position for blank duration 0 (-0.51°) was significantly different from that for all other blank durations, which did not differ from each other (range = -0.32° to -0.36°). There appeared to be no systematic relationship between saccade amplitude and mouse click position. For example, correlations between saccade amplitude and mouse click position (considered separately for each combination of saccade direction and saccade distance) were near 0 (all $r^2 < .03$) and a median split of the saccade amplitudes (again considered separately for each combination of saccade direction and saccade distance) revealed no significant differences in mouse click position between short and long saccades (all $p > .10$).

4.3. Discussion

The first two experiments showed that blanking helps the detection of backward displacements but not forward displacements. These results suggest that immediately after the saccade the saccade target is misremembered as being closer to the fixation point than it actually was. The effect of this is to make forward displacements relatively easier to detect because the position of the post-saccadic stimulus appears to be farther away from the remembered saccade target position than it actually was, and vice versa for backward displacements. Experiment 3 provides direct evidence that participants do indeed misremember the saccade target position as being closer to fixation under no-blank (0 ms duration) conditions. As blank duration increases the remembered saccade target position becomes more veridical, contributing to the detection of backward displacements. There appears to be a residual negative displacement bias (approximately 0.3°) in the remembered saccade target position at the longer blank durations, however. Because of this, detection of forward displacements is relatively unaffected by the shift in subjects' memory for the saccade target because its position is still remembered as being closer to the central fixation point than it actually was.

Although the results of this experiment provide support for the hypothesis that subjects misremember the position of the saccade target as being closer to fixation than it actually was under no-blank conditions, the small magnitude of this error (0.5°) and its time course suggest that it is not a complete explanation for the forward bias in displacement judgments. The mean bias in Experiment 1 (for the nine subjects whose data were fit well) was approximately 1.5° rather than 0.5°. Furthermore, the results of Experiment 2 indicate that it takes 50–100 ms for the forward bias to disappear, whereas the results of Experiment 3 show a bias only at 0 ms. These inconsistencies may be due to differences between the displacement perception paradigms and the ruler paradigm. Although judging displacement relies on memory for the position of the saccade target, other factors influence displacement perception as well, such as whether an onset or transient is perceived when the post-saccadic stimulus is presented (Deubel et al., 1996) and whether there is a perception of correspondence between the saccade target and the post-saccadic stimulus (Atsma, Majj, Koppen, Irwin, & Medendorp, 2016; Niemeier, Crawford, & Tweed, 2003, 2007; Tas et al., 2012). This latter factor in particular is missing from the ruler paradigm.

5. General discussion

Previous research has found that post-saccadic blanking improves

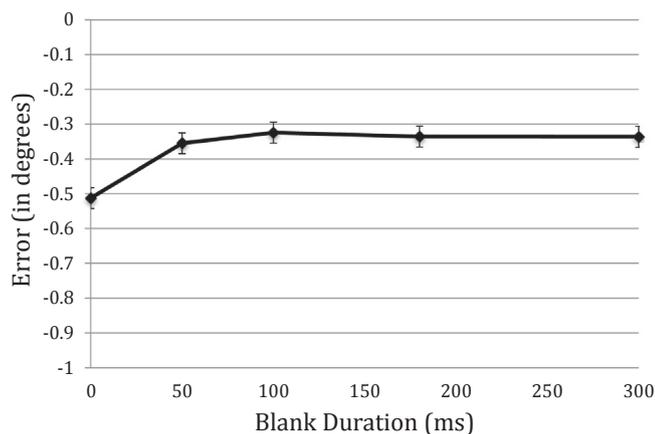


Fig. 6. Image of the ruler used for indicating report of the position of the saccade target in Experiment 3.

Table 3

Mean latency, duration, and amplitude of saccades as a function of saccade direction and saccade distance in experiment 3 (standard errors in parentheses).

	Latency 6°	Duration 6°	Amplitude 6°	Latency 8°	Duration 8°	Amplitude 8°
Left	250 (22.3)	37 (1.4)	5.5 (0.13)	222 (17.2)	42 (1.3)	7.1 (0.19)
Right	246 (16.0)	37 (0.9)	5.3 (0.15)	234 (13.5)	41 (0.9)	6.8 (0.19)

**Fig. 7.** Mean mouse click position (in degrees) relative to the center of the saccade target as a function of blank duration. Error bars depict standard errors.

performance in a task that requires participants to judge the direction in which a stimulus has been displaced across a saccade (Demeyer et al., 2010; Deubel et al., 1996, 1998; Tas et al., 2012), but hurts performance in a task that requires participants to judge whether a stimulus has been displaced or not across a saccade (Irwin & Robinson, 2015). These tasks differed in other ways as well, however, so the purpose of the present study was to compare the effect of post-saccadic blanking on displacement direction performance (which way did it move) and displacement detection performance (did it move or not) in the same experimental paradigm. This comparison allowed us to examine precisely how blanking improves the discrimination of displacements. Experiments 1 and 2 found that blanking improved performance in both kinds of tasks, but only for backward displacements and not forward displacements. The results of Experiment 3 suggest that this is due in part to subjects misremembering the position of the saccade target as being closer to central fixation when no blank separates saccade target offset and the presentation of the post-saccadic stimulus. The detection of backward displacements under blank conditions is also facilitated by greater spatial resolution for the post-saccadic stimulus (compared to forward displacements) and by the fact that a backwardly-displaced stimulus often appears in the opposite visual field from the saccade target.

The present findings are mostly consistent with the hypothesis of Deubel and colleagues (Deubel & Schneider, 1994; Deubel et al., 1996, 1998) that precise information about eye position and accurate memory for the position of the pre-saccadic target are available after a saccade and can be used to compensate for changes in the retinal position of the saccade target as long as these sources of information are not overridden by the presence of visual context (i.e., the post-saccadic target stimulus) immediately after the saccade. The results of the present experiments reveal that one refinement to the proposal of Deubel and colleagues is needed, however, and that is that the pre-saccadic target position is misremembered as being closer to central fixation than it actually is immediately after the saccade and more precise information about its position becomes available after a short delay. This refinement is consistent with other studies that have suggested that the eye position signal lags behind the eye movement itself by some period of time (e.g.,

Honda, 1993; Matin, 1976, 1986; Matin & Pearce, 1965; Ross et al., 1997).

As in the experiments of Irwin and Robinson (2015), Experiments 1 and 2 of the current paper found that blanking increased the false alarm rate (i.e., “move” responses when the target did not move) compared to no-blank trials. It seems clear that visual context (i.e., the presence of the post-saccadic stimulus when the eyes land and no blank is present) immediately after a saccade overrides other potential sources of information and biases subjects to perceive stability (lack of displacement) across saccades under no-blank conditions. The false alarm rate is very low under these circumstances because subjects perceive the stimulus to be present continuously and they assume that it did not move (MacKay, 1973; Matin et al., 1982). When a blank is present, however, then the perception of stimulus continuity is broken and other sources of information such as eye position information and memory for the pre-saccadic target position are consulted. The increase in false alarms under blank conditions indicates that memory for the pre-saccadic target position is not completely accurate even when a blank separates saccade target offset and post-saccadic stimulus presentation. The results of Experiment 3 support this conclusion as well, by showing a persistent error in subjects’ memory of the saccade target position across blank durations. The effect of this is that subjects perceive that the post-saccadic stimulus has been displaced even when it has not, leading to a high false alarm rate.

It seems likely that detection of displacement direction and the detection of displacement per se might be differentially sensitive to this kind of error. As noted earlier, when there is no blank in the move/no-move condition subjects perceive the stimulus to be present continuously and they assume that it did not move; when a blank is present, however, object continuity is broken and a small error in subjects’ memory for the initial saccade target location might lead them to judge (incorrectly) that the post-saccadic stimulus had been displaced. In contrast, in the forward/backward condition the subjects know that they will always have to judge the direction of displacement, so a small error in their memory for the initial saccade target location might have only a small effect on their ability to judge in which direction it had moved. Thus, blanking might be found to hurt the detection of displacement per se because of an increase in false alarms, while having minimal or beneficial effects on judging the direction of any displacement that does occur. Our results are consistent with this hypothesis, in that we found that blanking increased the proportion of “move” responses more than the proportion of “forward” responses in Experiments 1 and 2.

In the current experiments there were beneficial effects of blanking despite the increased false alarm rate in the move/no-move task. Given that blanking improved both displacement direction performance and displacement detection performance in the current experiments, one wonders why Irwin and Robinson (2015) found that blanking interfered with displacement detection in their experiments. The procedure used by Irwin and Robinson (2015) was different in several ways from the one used in the current experiments (and in Demeyer et al., 2010; Deubel et al., 1996, 1998; and Tas et al., 2012). In the current experiments only one stimulus (the saccade target) was presented, all saccades were horizontal, and subjects judged whether the saccade target moved or not across the saccade. In contrast, in the experiments of Irwin and Robinson (2015), multiple stimuli were presented on each

trial, the stimuli were presented on virtual concentric circles centered on the initial fixation point (so that saccades of varying angular eccentricities had to be made), and on some trials the saccade target was probed while on other trials another item in the array was probed. We presume that one or more of these differences led to the differences across studies.

Our results show that blanking improves the detection of displacement as well as the detection of displacement direction across saccades, at least for backward displacements. Blanking is not the only factor that improves the perception of stability across saccades, however. Others have shown that changing the features of the saccade target, such as its polarity, shape, or orientation, also improves perception across saccades (e.g., Demeyer et al., 2010; Poth, Herwig, & Schneider, 2015; Tas et al., 2012; Zimmermann, Born, Fink, & Cavanagh, 2014), indicating that object correspondence is an important contributor (see also Atsma et al., 2016). Visual factors that affect the quality of the representation of the saccade target per se, such as contrast (Matsumiya, Sato, & Shioiri, 2016), preview duration (Zimmermann et al., 2013) and size (Zimmermann, 2016) also affect displacement perception across saccades, however. Given the range of factors that have been shown to influence the perception of stability across saccades, it seems likely that multiple mechanisms contribute to this outcome (Demeyer et al., 2010; Zimmermann et al., 2014).

Author contributions

David Irwin contributed data analysis, writing, and editing. Maria Robinson performed the programming and contributed to the writing and editing. Both authors contributed to the concept for the study and approved the final version of the manuscript for submission.

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