



Contrast dependence of saccadic blanking and landmark effects



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ABSTRACT

Two phenomena have been reported to affect the perceived displacement of a visual target during saccadic eye movements: the blanking effect and landmark effect. In the blanking effect, temporarily blanking the target after a saccade improves displacement judgments. In the landmark effect, illusory target displacement occurs when a continuously presented landmark is displaced during a saccade, and the target is temporarily blanked after the saccade without displacement. We show that the strengths of the blanking and landmark effects vary with stimulus contrast. In the blanking effect, target displacement detection rate increased with luminance contrast of the target. In the landmark effect, illusory target displacement decreased with luminance contrast of the target. Moreover, the landmark effect was found even for stimuli without luminance contrast (equiluminant color stimuli), while the blanking effect disappeared. These results can be attributed to a reduction in sensitivity of target displacement by a reduction of luminance contrast, which suggests that changes in luminance, or transient signals, play a critical role in visual stability across saccades.

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1. Introduction

Saccadic eye movements cause the image of the visual world to shift on the retina, intermittently disrupting retinal image stability. Despite this instability, we perceive the visual world as stable. How does the visual system achieve visual stability when retinal images are frequently displaced by saccades? One possibility is that the visual system assumes that the visual world does not change during saccades (Mackay, 1962). This assumption is supported by the inability to detect small displacements during saccades (Bridgeman, Hendry, & Stark, 1975), referred to as saccadic suppression of displacement, motion, or transient signals (Bridgeman et al., 1975; Burr, Morrone, & Ross, 1994; Shioiri & Cavanagh, 1989; Uchikawa & Sato, 1995). Consequently, the visual world appears stable and uninterrupted.

However, the mechanisms for visual stability across saccades involve more than saccadic suppression of displacement, as suggested by two phenomena influencing the perception of displacement during saccades. First, previous studies demonstrated that brief blanking of a target after a saccade produces a large improvement in displacement judgment (the ‘blanking effect’) in cases where the target moves to a new location during the saccade

(Deubel, Schneider, & Bridgeman, 1996, 2002). This suggests that postsaccadic target blanking may prevent saccadic suppression of image displacement. The blanking effect may reflect a general property of saccadic visual processing rather than an effect specific to displacement. A recent study reported that postsaccadic target blanking also facilitates spatial frequency discrimination (Weiss, Schneider, & Herwig, 2015), while another study reported that postsaccadic target blanking does not improve sensitivity for movements of an object (Gysen, Verfaillie, & De Graef, 2002). Second, previous studies have reported that a landmark presented near a stationary, temporarily blanked saccadic target induces an illusory target displacement if the landmark is displaced during the saccade (the ‘landmark effect’) (Deubel, 2004; Deubel, Bridgeman, & Schneider, 1998). Both the blanking and landmark effects involve a transient change in luminance. Thus, blanking the target after the saccade may activate motion- and/or transient-sensitive systems, which are usually suppressed by saccades. If this is true, the activation of the motion- and transient-sensitive systems could improve the accuracy of target displacement judgments (i.e., facilitate the blanking effect) and strengthen the target-related signals to reduce the illusory perception of target displacement induced by landmark displacement.

The magnocellular pathway, which responds preferentially to luminance transients or motion stimuli (Merigan, Byrne, & Maunsell, 1991; Schiller, Logothetis, & Charles, 1990), may be involved in saccadic suppression of image displacement as well

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as in the blanking and landmark effects. For instance, a previous study demonstrated that saccadic suppression of image displacement depends on luminance contrast and becomes stronger with luminance stimuli than with equiluminance chromatic stimuli (Bridgeman & Macknik, 1995), suggesting that the magnocellular pathway is selectively affected in saccadic suppression of image displacement. This implies that luminance contrast is important for perisaccadic perceptual phenomena, including the blanking and landmark effects. To our knowledge, however, no study has examined the effects of luminance contrast on the blanking effect and on the landmark effect.

In this study, we investigated the influence of target luminance contrast on the blanking effect (Experiment 1) and the landmark effect (Experiment 2). We also investigated the effect of contrast using equiluminant chromatic stimuli (Experiment 3). The purpose of the experiments was to examine the influence of transient signals caused by target blanking and reappearance after a saccade on each of these phenomena. If transient signals are crucial for displacement detection across saccades, we would expect that the strengths of the blanking and landmark effects would vary with luminance contrast, as higher contrast produces stronger transient signals. This study reports that the increase in the blanking benefit of target displacement with increasing target contrast for the blanking effect is similar to that for the landmark effect, and finds that the landmark effect occurs even for equiluminant chromatic stimuli.

2. Experiment 1: effect of target contrast on the blanking effect

2.1. Methods

2.1.1. Observers

Five male observers from 24 to 38 years old (mean age, 29 years) with normal vision participated in this study and gave informed consent in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Four of them were naive to the purpose of this study. The other subject was one of the authors (KM). This study was approved by the Ethics Committee of the Research Institute of Electrical Communication, Tohoku University.

2.1.2. Apparatus

The observer's head was fixed with a combination forehead and chin rest. Visual stimuli were presented on a CRT display (GDM-F520, Sony) with a refresh rate of 100 Hz. The viewing distance was 60 cm. The display subtended 38° high and 49° wide, and was controlled by a visual stimulus generator (ViSaGe, Cambridge Research Systems).

A limbus-tracking device (T.K.K.2930a, Takei Scientific Instruments Co., Ltd.) consisting of an infrared-emitting diode and two photodiodes was used to measure horizontal movements of the observer's right eye. The analog signal from the device was digitized at a sampling rate of 100 Hz and recorded on a computer. We differentiated the trajectory of the eye position to obtain the velocity of eye movement. The onset of a saccade was defined as the time at which eye velocity exceeded 30°/s. Saccade latency was defined as the period between the onset of target and the onset of saccade.

2.1.3. Calibration of eye movement

Each session started with a calibration procedure where the observer fixated on five dots presented sequentially on a horizontal center line of the display and pushed a button after each fixation was completed. Horizontal eye positions were expressed as volt-

ages when the button was pushed. A linear regression procedure determined the relationship between voltage and dot position.

2.1.4. Stimuli

Fig. 1 shows the arrangement of visual stimuli in Experiment 1. First, a circular fixation cue (0.4° in diameter, 27.4 cd/m²) was presented 4° to the left of the display center. The saccadic target, which was the same as the fixation cue, was presented 4° to the right of the center. The luminance of the saccadic target varied randomly between set values of 24.0, 25.1, 27.4, 32.0, and 41.1 cd/m² from trial to trial, while background luminance was constant at 22.8 cd/m². Thus, the contrast of the saccadic target varied randomly between 5%, 10%, 20%, 40%, and 80%.

The color of the stimuli was yellow [CIE x, y chromaticity coordinates: 0.401, 0.518].

2.1.5. Procedure

Fig. 1 shows the stimulus sequence of a blanking effect trial. Initially, a fixation point was presented 4° to the left of the display center. The observer fixated on the fixation point and pressed a button to start the trial. After a randomly selected delay between 500 and 1300 ms, the fixation point was extinguished and the saccadic target appeared 4° to the right of the display center, with variable luminance contrast. The observer was instructed to make a saccade toward this target as quickly as possible. In the 'blank' condition, the target was blanked for 100 ms after onset of the saccade (Fig. 1a). When the target reappeared, it was displaced by 0.15° to the left or right. The target was extinguished 200 ms after it reappeared. In the 'no blank' condition (Fig. 1b), the target was continuously present, but was displaced 0.15° to the left or right just after the saccade onset. In these 'no blank' trials, the target was extinguished 300 ms after displacement. The observer reported whether the target was displaced to the left or to the right. Each observer performed four sessions. Each session consisted of 50 trials of the 'blank' condition and 50 trials of the 'no blank' condition. Trials were excluded from analysis if saccade latency was shorter than 120 ms or longer than 400 ms, or if the blanking of the target occurred after saccade offset. Across participants, saccade latency was shorter than 120 ms or longer than 400 ms in 2.84% of trials, and the blanking of the target occurred after the saccade offset in 2.75% of trials; thus, less than 6% of trials were excluded from the analysis.

2.2. Results and discussion

Fig. 2 shows the percentages of correct displacement discriminations as a function of target contrast. The solid and open symbols represent the 'blank' and 'no blank' conditions, respectively. Fig. 2a–e present the responses of each observer, and Fig. 2f shows the mean data of all five observers. Discrimination of target displacement improved progressively with increasing target contrast in the 'blank' condition. In the 'no blank' condition, however, discrimination of target displacement improved only slightly with increasing target contrast. The improvement of discrimination of target displacement by a target blank at a high contrast is consistent with previous findings (Deubel et al., 1996, 2002). Repeated measures analysis of variance (ANOVA) of group mean data with two presentation conditions ('blank' and 'no blank') and five contrast levels (5%, 10%, 20%, 40%, and 80%) revealed significant main effects of presentation condition [$F(1, 4) = 28.29, p < 0.01$] and contrast level [$F(4, 16) = 20.28, p < 0.001$]. There was also an interaction between presentation condition and contrast level [$F(4, 16) = 3.94, p < 0.05$]. The results suggest that the blanking effect depends on target contrast and grows in strength as the contrast of the target increases.

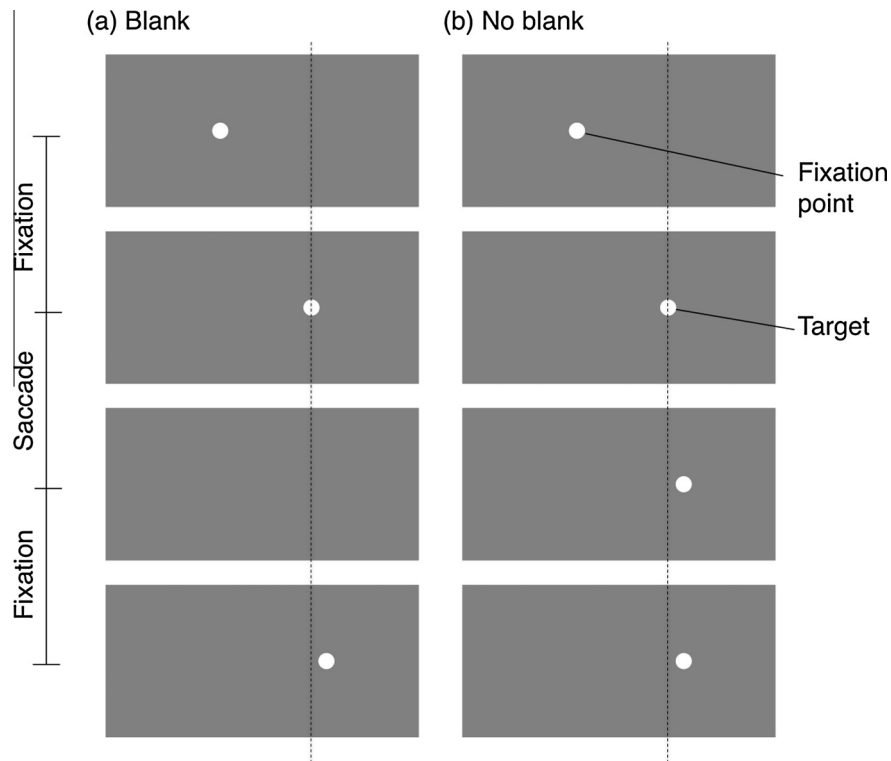


Fig. 1. Arrangement of visual stimuli and stimulus sequence in Experiment 1. (a) Blank condition. (b) No blank condition. First, an observer fixated on the fixation point, then pressed a button. After a waiting period of 500–1300 ms, the target was presented 4° to the right of the display center. The observer made a saccade toward the target as soon as possible. In the 'blank' condition, when the saccade started, the target was extinguished (left panel). At 100 ms after the saccade, the target appeared again, displaced by 0.15° to the left or right. In the 'no blank' condition, the target was continuously present and the target was displaced 0.15° to the left or right when the saccade started (right panel). After a delay of 200 ms, all stimuli were extinguished.

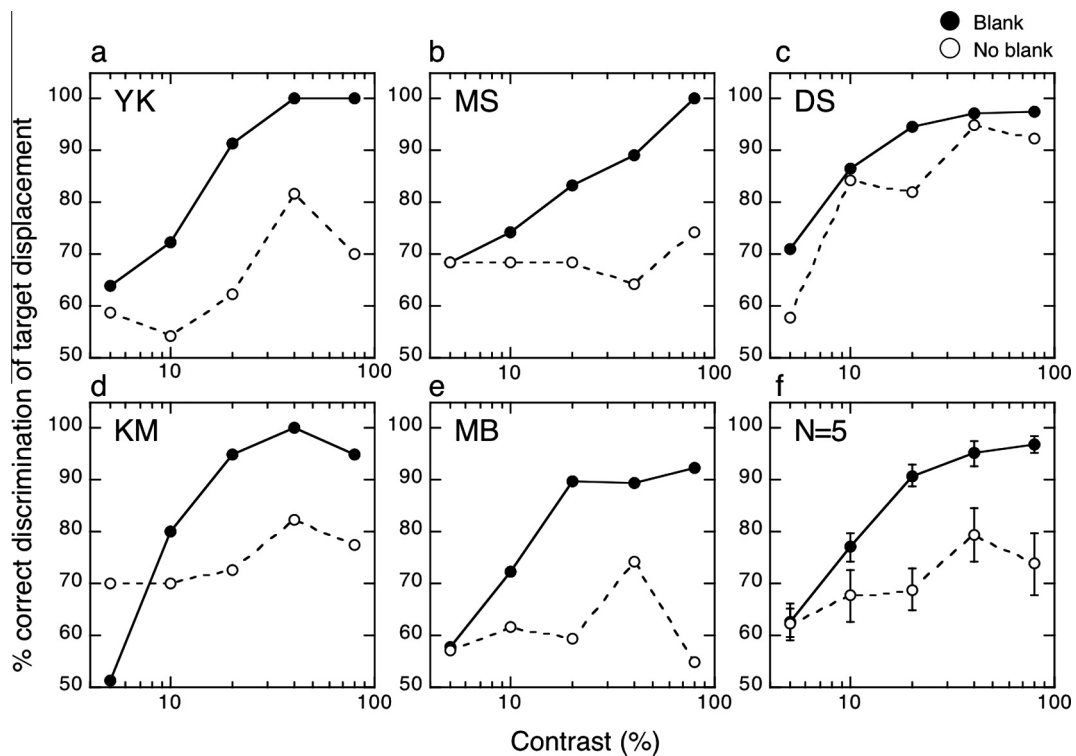


Fig. 2. Results of Experiment 1. The graphs show the percentages of correct displacement discrimination as a function of luminance contrast. Solid and open symbols represent the 'blank' condition and the 'no blank' condition, respectively. (a–e) Results for each observer. (f) The means of all five observers. Error bars represent the standard error of the mean.

We also analyzed the influence of target contrast on saccade latency and accuracy. Fig. 3a and b show mean saccade latencies and saccade accuracies, respectively, as a function of target contrast. Saccade accuracy was defined as an error in saccade end position from the saccade target. The solid and open symbols represent the ‘blank’ and ‘no blank’ conditions, respectively. For saccade latencies, ANOVA revealed a significant main effect of contrast level [$F(4, 16) = 82.49, p < 0.0001$]. However, there was no significant main effect of presentation condition (‘blank’ and ‘no blank’) [$F(1, 4) = 0.12, n.s.$], and no interaction between presentation condition and contrast level [$F(4, 16) = 2.32, n.s.$]. For saccade accuracy, ANOVA revealed no significant main effect of contrast level [$F(4, 16) = 1.34, n.s.$] or presentation condition (‘blank’ and ‘no blank’) [$F(1, 4) = 0.0002, n.s.$], and no interaction between presentation condition and contrast level [$F(4, 16) = 0.67, n.s.$]. Although target contrast had an effect on saccade latency, saccade latency and accuracy are not related to the difference between the blank and no-blank conditions, and are not considered in our analysis.

3. Experiment 2: effect of target contrast on the landmark effect

Experiment 2 examined whether the landmark effect was influenced by the contrast of the blanked target. In the landmark effect, a landmark displaced near a stationary blanked saccade target induces an illusory target displacement (Fig. 4a). If the illusory displacement of the target is related to the strength of the transient signal from target blanking/reappearance after the saccade, it should be reduced (i.e., the target localized more accurately) by an increase in target contrast. With high contrast, therefore, the target should tend to appear stationary across the saccade even in the presence of a displaced landmark.

3.1. Methods

Five male observers from 24 to 38 years old (mean age, 30.6 years) with normal vision participated in this study and gave informed consent in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Four of them were naive to the purpose of this study while the fifth was one of the authors (KM).

Fig. 4 shows the arrangement of visual stimuli. A circle (0.4° in diameter, 27.4 cd/m^2) was presented 4° to the left of the display center as the fixation cue. The saccadic target (circle; 0.4° in diameter) and a landmark (rectangle; 0.4° in height and 0.4° in width) were presented 4° to the right of the center, with the landmark 0.5° above the saccadic target. The luminance of the saccadic target was varied in the same way as in Experiment 1, and the luminance of the background was the same as in Experiment 1. Thus, the contrast of the saccadic target was varied between set values of 5%, 10%, 20%, 40%, and 80%. The luminance of the landmark was constant at 24.0 cd/m^2 . The contrast of the landmark was constant at 5% relative to the background. The color of all stimuli was yellow.

Fig. 4 shows the stimulus sequence for a trial. The observer fixated on the fixation point and pressed a button to start the trial. After a randomly selected delay between 500 and 1300 ms, the fixation point was extinguished and the saccadic target appeared 4° to the right of the display center. The luminance contrast of the target was chosen randomly from a set of predefined values of 5%, 10%, 20%, 40%, and 80%. The observer made an 8° rightward saccade toward the target as quickly as possible. After the onset of the saccade, the target was blanked for 100 ms while the landmark remained present. In the ‘landmark displacement’ condition, the landmark was displaced by 0.25° to the left or right just after saccade onset (Fig. 4a). At 100 ms after saccade onset, the target reappeared at the same position as before. In the ‘target displacement’ condition, the target was displaced by 0.25° to the left or right when it reappeared, while the landmark remained stationary (Fig. 4b). All stimuli were extinguished 200 ms after the target reappeared. The observer reported whether the target or the landmark was displaced. Each observer performed two sessions, and each session consisted of 50 trials of the ‘landmark displacement’ condition and 50 trials of the ‘target displacement’ condition, selected at random. Trials were excluded from analysis if the saccade latency was shorter than 120 ms or longer than 400 ms, or if the blanking of the target occurred after the saccade offset. Across participants, the saccade latency was shorter than 120 ms or longer than 400 ms in 5.4% of trials, and the blanking of the target occurred after the saccade offset in 0% of trials; thus, less than 6% of trials were excluded from analysis.

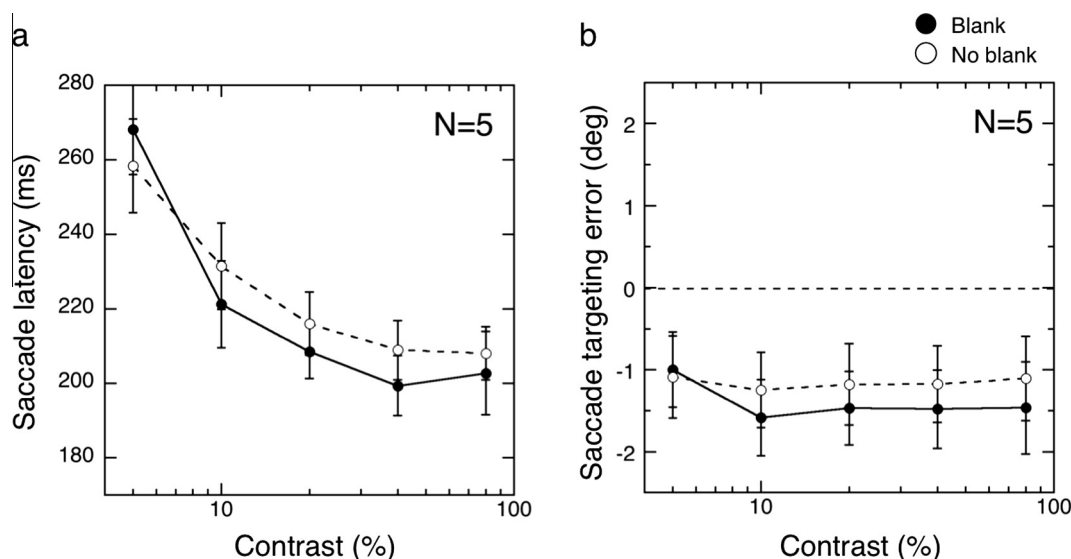


Fig. 3. Effects of target contrast on saccade latency and accuracy in Experiment 1. (a) Saccade latency as a function of target luminance contrast. (b) Saccade targeting error as a function of target luminance contrast. Solid and open symbols represent the ‘blank’ and ‘no blank’ conditions, respectively. The graphs show the means of all five observers. Error bars represent the standard error of the mean.

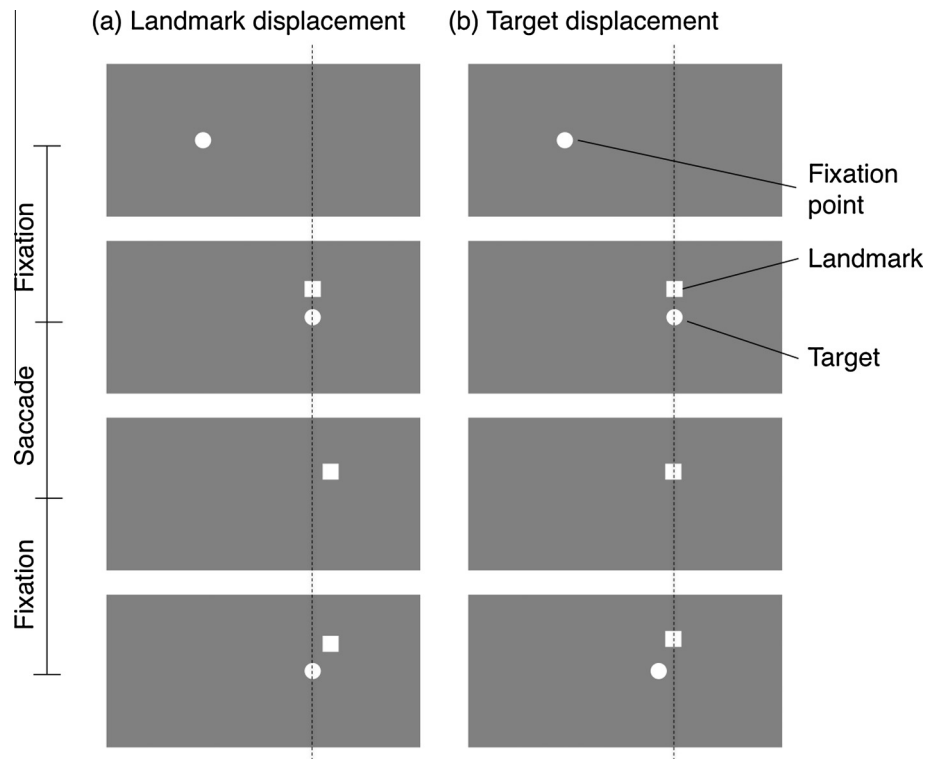


Fig. 4. Arrangement of visual stimuli and stimulus sequence in Experiment 2. (a) Landmark displacement condition. (b) Target displacement condition.

3.2. Results and discussion

Fig. 5 shows the percentages of trials in which observers reported target displacement as a function of target contrast in

the landmark displacement condition (solid symbols) and in the target displacement condition (open symbols). Fig. 5a–e show the individual results of each observer and Fig. 5f shows the means of all five observers. When the contrast of the target was low

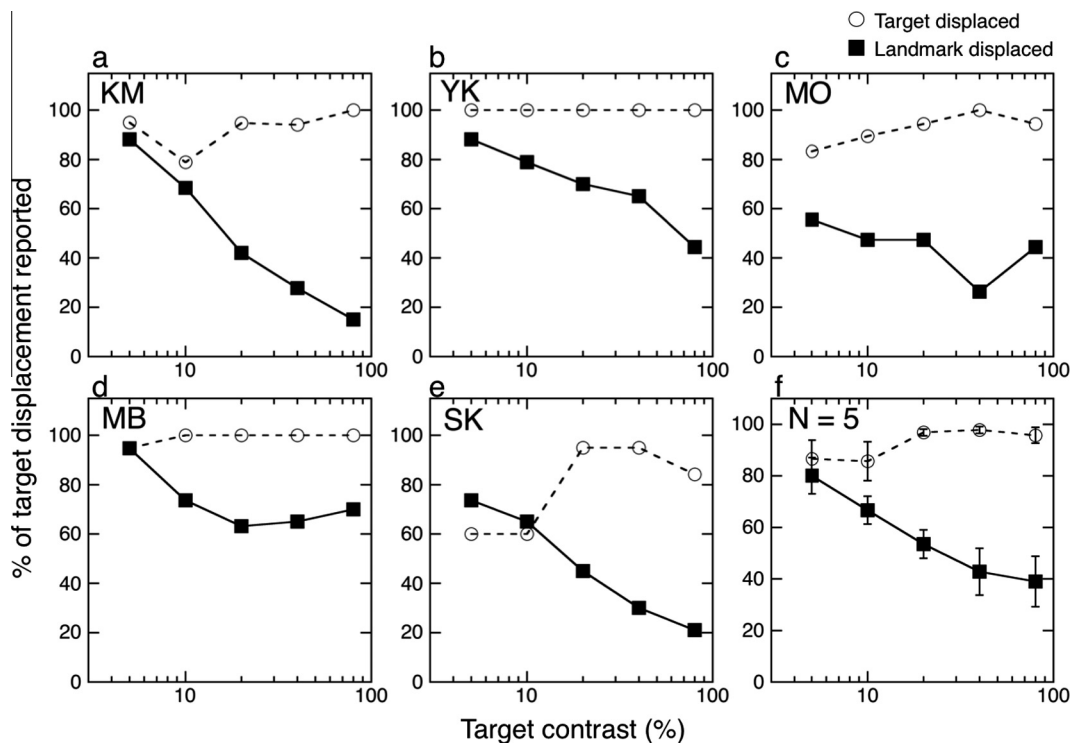


Fig. 5. Results of Experiment 2. The graphs show the percentage of target displacement reported as a function of luminance contrast. Open circle and solid square symbols represent the target displacement and landmark displacement conditions, respectively. (a–e) Results for each observer. (f) The means of all five observers. Error bars represent the standard error of the mean.

(5%), observers consistently perceived an illusory displacement of the target in the landmark displacement condition, and judgment of target stability/displacement was comparable to that in the target displacement condition, consistent with previous findings (Deubel, 2004; Deubel et al., 1998). Performance improved progressively (i.e., the landmark effect weakened) with increasing target contrast. On the other hand, the report in the target displacement condition was almost always correct, even for low target contrast. ANOVA of the group mean data revealed significant main effects of displacement condition ('landmark' and 'target') [$F(1, 4) = 25.06, p < 0.005$] and contrast level [$F(4, 16) = 4.06, p < 0.01$]. There was also an interaction between displacement condition and contrast level [$F(4, 16) = 13.55, p < 0.0001$]. These results suggest that, in the presence of a continuous landmark, observers tend to attribute landmark displacements to the target, and that this landmark effect is stronger when the contrast of the target is low.

We also analyzed the influence of target contrast on saccade latency and accuracy. Fig. 6a and b show mean saccade latencies and saccade accuracies, respectively, as a function of target contrast. Saccade accuracy was defined as an error in the distance of the saccade endpoint from the saccade target. The solid and open symbols represent the 'landmark displacement' and 'target displacement' conditions, respectively. For saccade latencies, ANOVA revealed a significant main effect of contrast level [$F(4, 16) = 33.89, p < 0.0001$], but there was no significant main effect of presentation condition ('landmark' and 'target') [$F(1, 4) = 0.20, n.s.$], and no interaction between presentation condition and contrast level [$F(4, 16) = 0.52, n.s.$]. For saccade accuracy, ANOVA revealed no significant main effect of presentation condition [$F(4, 16) = 0.10, n.s.$] or contrast level [$F(4, 16) = 1.44, n.s.$], and no interaction between presentation condition and contrast level [$F(4, 16) = 0.55, n.s.$]. Although target contrast had an effect on saccade latency, saccade latency and accuracy therefore cannot explain the difference between the 'landmark displacement' and 'target displacement' conditions, and are not considered further in our analysis.

To compare the influence of luminance contrast on the blanking and landmark effects, we analyzed the sensitivity (d') and the bias of the decision criterion (λ) using procedures from signal detection theory (SDT; see Fig. 7f) (Wickens, 2002). For the blanking effect

(Experiment 1), a correct report for the right (or left) displacement of the target was defined as a hit, and an incorrect report for the left (or right) displacement of the target (a false response) was defined as a false alarm. Using the hit and false-alarm rates, we calculated d' for the blank and no-blank conditions (Fig. 7a). Similarly, for the landmark effect (Experiment 2), a correct report for target displacement (i.e., correctly attributing the displacement to the target) was defined as a hit, and an incorrect report for landmark displacement (i.e., incorrectly attributing the displacement to the target) was defined as a false alarm. d' was calculated from these hit and false-alarm rates as the blank condition for the landmark-effect experiment (Fig. 7b). In order to estimate the effect of blanking on landmark effect, we used data from the no-blank condition of a landmark-effect experiment performed in a previous study (Deubel et al., 1998) (Fig. 7b). In that study, the detection rate was very low even for a target contrast of 88%, and we assumed that d' for the no-blank condition would be constant for lower target contrasts. We then defined a blanking benefit index as the difference in d' between the blank and no-blank conditions, for both the blanking and landmark effects (Fig. 7c). This allowed us to compare the effect of target blanking between Experiment 1 and Experiment 2 (i.e., between the blanking and the landmark effects) even though the task was different between these experiments. For both the blanking effect and the landmark effect, the blanking benefit reflects the effect of a target blank. Fig. 7c shows that blanking benefit increases similarly with target contrast for both the blanking and the landmark effects. Fig. 7d shows that the benefit due to target blanking in Experiment 1 is significantly correlated with that of the landmark effect studied in Experiment 2 [$r^2 = 0.33, t(23) = 3.37, p < 0.005$]. In Fig. 7d, open symbols represent different observers with different contrasts. The data were fitted with a least-squares regression line. This correlation suggests that the blanking and landmark effects are influenced by a common mechanism that improves veridical displacement detection with target contrast, but only if there is a target blank.

We also analyzed the bias of the decision criterion, which can be indexed by the quantity λ (Wickens, 2002)—a value representing the position of the criterion relative to a point halfway between the signal and noise distributions (Fig. 7e). A value of zero indicates that the criterion is at the point halfway between the peaks of the signal and noise distributions and that there is no bias in the

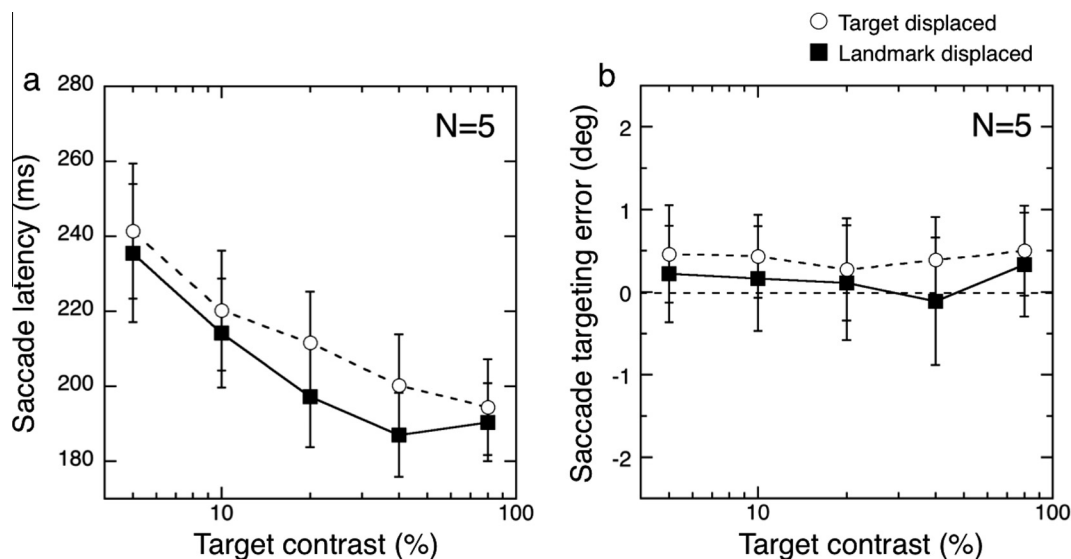


Fig. 6. The effects of target contrast on saccade latency and accuracy in Experiment 2. (a) Saccade latency as a function of target luminance contrast. (b) Saccade targeting error as a function of target luminance contrast. Solid and open symbols represent the 'landmark displacement' condition and the 'target displacement' condition, respectively. The graphs show the means of all five observers. Error bars represent the standard error of the mean.

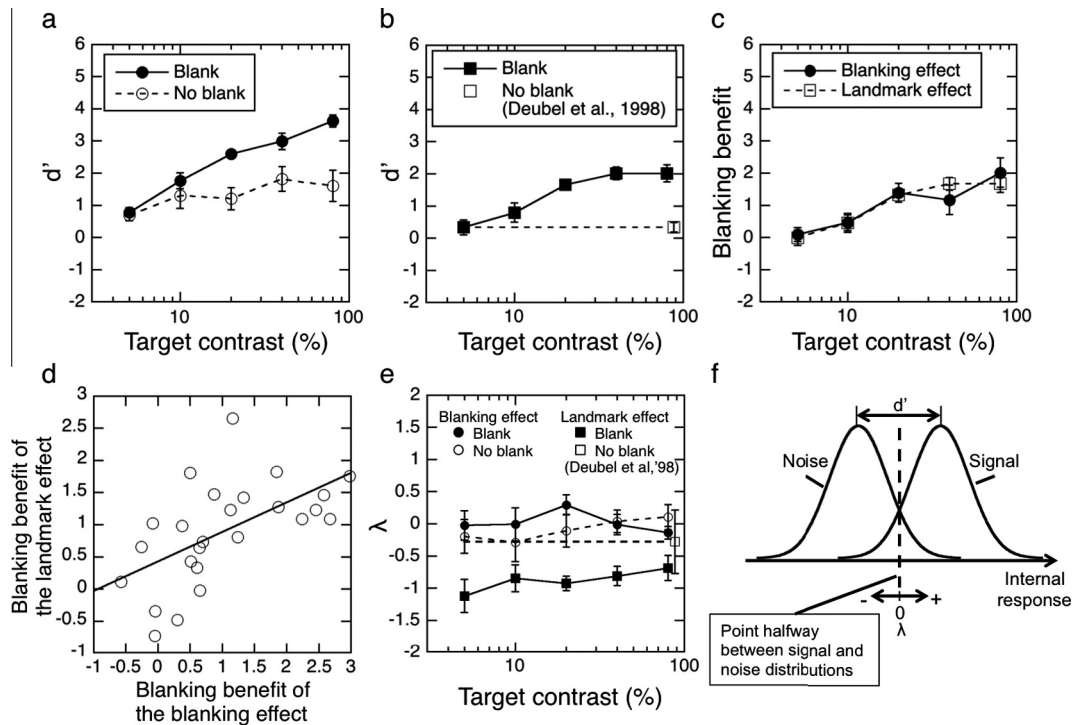


Fig. 7. d' , blanking benefit, and bias of the decision criterion. The data were analyzed using procedures from signal detection theory. (a) d' as a function of target luminance contrast for the blanking effect. Solid circle and open circle symbols represent the blank and no-blank conditions, respectively. (b) d' as a function of target luminance contrast for the landmark effect. We used data from a previous study (Deubel et al., 1998) as results for the no-blank condition. Solid square and open square symbols represent the blank and no-blank conditions, respectively. (c) Blanking benefit as a function of target luminance contrast. The difference in d' between the blank and no-blank conditions is defined as an index of the benefit due to target blanking. Solid circle and open square symbols represent the data for the blanking and landmark effects, respectively. (d) Correlation between the blanking benefits of Experiment 1 (blanking effect) and Experiment 2 (landmark effect). Open circle symbols represent different observers with different contrasts. The data are fitted with a least-squares regression line. (e) λ as a function of target luminance contrast. The quantity λ indexes the bias of the decision criterion. Solid circle and open circle symbols represent the blank and no-blank conditions, respectively, in the 'blanking effect' trials. Solid square and open square symbols represent the blank and no-blank conditions, respectively, in the 'landmark effect' trials. Note that the data from the previous study (Deubel et al., 1998) are used as results for the no-blank condition in the 'landmark effect' trials. (f) Illustration of d' and λ . Error bars represent the standard error of the mean.

response. Fig. 7e shows that λ calculated using the data from the blanking-effect experiment (Experiment 1) is approximately zero across all target contrasts for the blank and no-blank conditions; that is, there is no decision bias, independent of target contrast for the blanking-effect experiment. Note that the positive value of λ indicates a rightward direction independent of displacement direction, and the values for the right and left displacement signal trials were averaged after independent analyses. However, for the landmark-effect experiment (Experiment 2), λ has an approximately constant negative value across all target contrasts (Fig. 7e). The negative λ indicates that the decision criterion is biased toward the peak of the noise distribution, which corresponds to the landmark displacement; that is, the negative λ corresponds to the landmark effect. We also calculated λ using the data from the no-blank condition of the landmark-effect experiment from Deubel et al. (1998). This λ was very close to zero, indicating that the decision criterion was biased only if there was a target blank. ANOVA for λ revealed no significant main effect of contrast level for the blanking-effect and landmark-effect experiments [$F(4, 16) = 1.88$, *n.s.* for the blanking-effect experiment; $F(4, 16) = 0.41$, *n.s.* for the landmark-effect experiment]. These results suggest that the bias of the decision criterion, which corresponds to the attribution of the landmark displacement to the target displacement, is independent of target contrast.

Bonferroni-corrected paired t -tests for multiple comparisons revealed significant differences between the blanking-effect and landmark-effect experiments [$t(4) = -1.15$, $p < 0.001$ for the blank condition in the blanking-effect experiment; $t(4) = -1.04$, $p < 0.001$ for the no-blank condition in the blanking-effect experi-

ment], while there was no significant difference between the blank and no-blank conditions in the blanking-effect experiment [$t(4) = -0.11$, *n.s.*] and both values for these conditions were close to zero, as shown in Fig. 7e. Thus, the bias λ is important for characterizing the landmark effect but not the blanking effect.

In the original experiment, we varied the contrast of the target only, and used a fixed contrast value of 5% for the landmark. Hence, it is not clear whether the influence of contrast on the landmark effect was caused by the relationship between the target and background, or between the target and landmark. Therefore, we conducted two additional experiments to address this issue. In the first additional experiment, the contrasts of the saccadic target and the landmark were always the same and chosen from set values of 5%, 10%, 20%, 40%, and 80%. In this experiment, the influence of contrast on the landmark effect was similar to that in the original experiment (compare Figs. 5f and 8a). ANOVA of the group means revealed significant main effects of displacement condition ('landmark' and 'target') [$F(1, 5) = 106.5$, $p < 0.0001$] and contrast level [$F(4, 20) = 10.54$, $p < 0.0001$]. There was also an interaction between displacement condition and contrast level [$F(4, 20) = 4.72$, $p < 0.001$]. In the second additional experiment, the contrast of the landmark was chosen from set values of 5%, 10%, 20%, 40%, and 80%, while the contrast of the saccadic target was constant at 5%. The results show that the contrast of the landmark did not significantly influence the landmark effect (Fig. 8b). ANOVA of the group means revealed no significant main effects of displacement condition ('landmark' and 'target') [$F(1, 4) = 2.45$, $p = 0.16$ *n.s.*] and contrast level [$F(4, 16) = 1.16$, $p = 0.35$ *n.s.*]. Furthermore, there was no interaction between displacement condition and con-

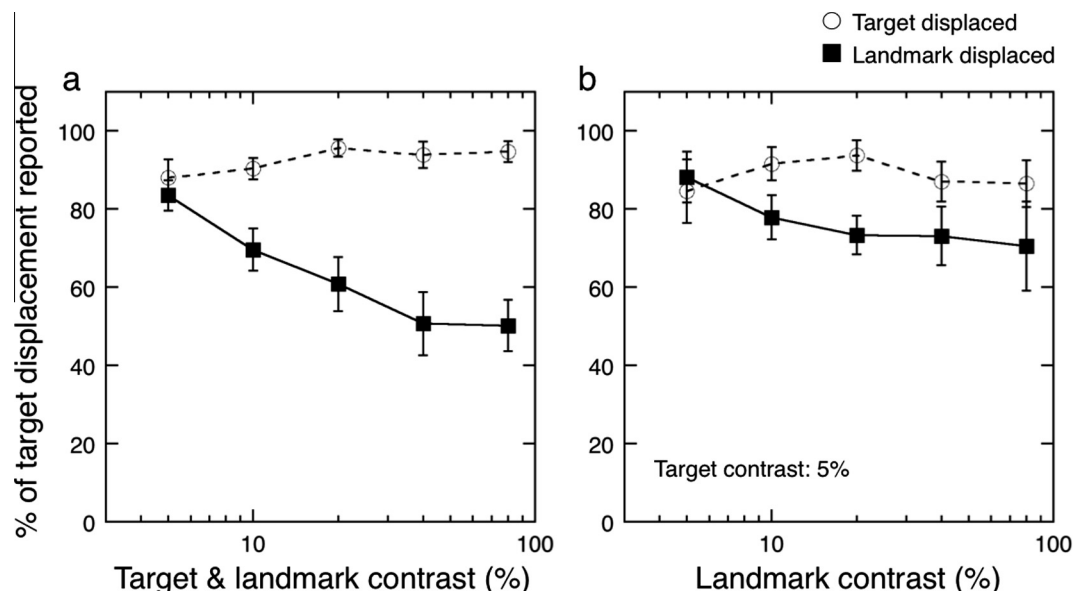


Fig. 8. Influence of the contrasts of the target and the landmark for the landmark effect. The graphs show the percentage of trials reporting target displacement as a function of luminance contrast. Open circle and solid square symbols represent the target displacement and the landmark displacement conditions, respectively. Error bars represent the standard error of the mean. (a) Target and landmark contrast change. The contrasts of the target and landmark were always the same. $N = 6$. (b) Landmark contrast change. The contrast of the target was constant at 5%. $N = 5$.

trast level [$F(4, 16) = 2.29$, $p = 0.08$ n.s.]. These results suggest that the effect of contrast found in the original experiment can be attributed to the effect of target contrast alone.

4. Experiment 3: equiluminant chromatic stimuli

Experiment 1 revealed that the blanking effect was stronger when the contrast of the blanked target was *high*. Experiment 2 demonstrated that the landmark effect was stronger when the contrast of the blanked target was *low*. These results suggest that luminance-based transient signals from target blanking/reappearance after a saccade may facilitate the blanking effect and inhibit the landmark effect. If this is true, the landmark effect should still occur with equiluminant stimuli, while the blanking effect should not. Therefore, we performed a third experiment that examined whether the blanking effect and the landmark effect would also occur with equiluminant chromatic stimuli.

4.1. Methods

The same five observers as in Experiment 1 participated in this experiment. Visual stimuli were equiluminant chromatic objects with a fixed luminance of 22.8 cd/m^2 . The background was red, and the target and landmark were green [CIE x, y chromaticity coordinates: 0.625, 0.344 for red; 0.286, 0.608 for green]. Each color was produced by one phosphor of the CRT monitor. An equiluminant level for the red and green CRT phosphors was determined for each observer using heterochromatic modulation photometry at 15 Hz (Pokorny, Smith, & Lutze, 1989).

For the 'blanking effect' condition, the procedure was the same as in Experiment 1. Each observer performed two sessions, and each session consisted of 40 trials of the 'blank' condition and 40 trials of the 'no blank' condition. For the 'landmark effect' condition, the procedure was the same as in Experiment 2. Each observer performed two sessions, each consisting of 40 'landmark displacement' trials and 40 'target displacement' trials. Trials were excluded from analysis if the saccade latency was shorter than 120 ms or longer than 400 ms, or if the blanking of the target

occurred after the saccade offset. Across participants, the saccade latency was shorter than 120 ms or longer than 400 ms in 8.4% of trials, and the blanking of the target occurred after the saccade offset in 0.06% of trials; thus, less than 9% of trials were excluded from the analysis.

4.2. Results and discussion

Fig. 9a and b show the percentages of correct displacement discriminations for the 'blanking effect' condition. In Fig. 9a, the black and gray bars represent the 'blank' and 'no blank' conditions, respectively. In Fig. 9b, the horizontal and vertical axes represent performance for the 'blank' and 'no blank' conditions, respectively. The open symbols show the results of each observer and the solid symbol shows the means of all five observers. In contrast to Experiment 1, discrimination of target displacement in the 'blank' condition did not improve compared with the 'no blank' condition (Fig. 5f), and ANOVA of the group mean data indicated no significant effect of presentation condition ('blank' and 'no blank') [$F(1, 4) = 0.006$, $p = 0.94$ n.s.]. Thus, the blanking effect did not occur for equiluminant stimuli.

Fig. 9c and d show the percentages of trials reporting target displacement for the 'landmark effect' condition. In Fig. 9c, the black and gray bars represent the 'landmark displacement' and 'target displacement' conditions, respectively. In Fig. 9d, the horizontal and vertical axes represent performance for the 'landmark displacement' and 'target displacement' conditions, respectively. The open symbols show the results of each observer and the solid symbol shows the means of all five observers. These findings indicate that observers still perceived an illusory displacement of the target in the landmark displacement condition. A t -test of the group mean data confirmed that the percentage of trials reporting target displacement for each condition was significantly larger than 0 [$t(4) = 33.81$, $p < 0.0001$ for the landmark displacement condition; $t(4) = 25.24$, $p < 0.0001$ for the target displacement condition], indicating that the landmark effect occurs even when stimuli are equiluminant chromatic objects. ANOVA on the group mean data revealed a significant main effect of displacement condition ('land-

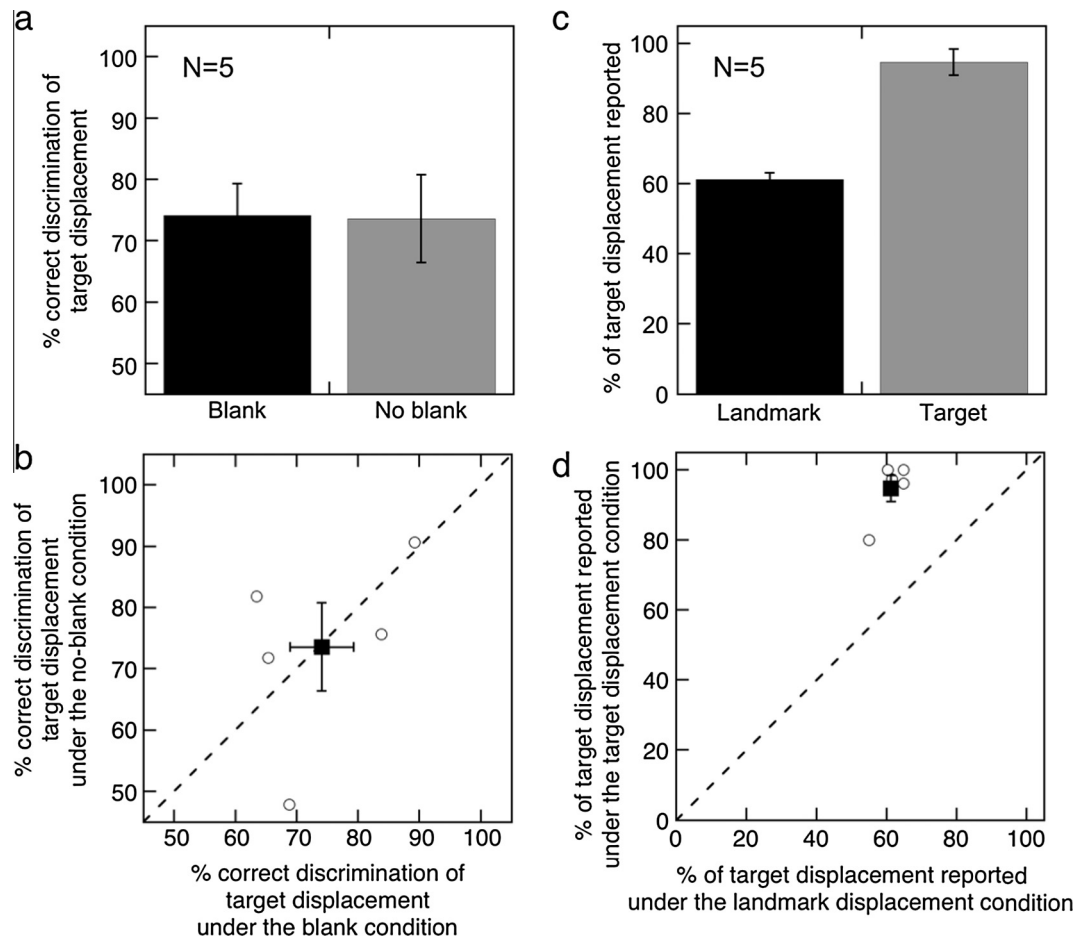


Fig. 9. Results of Experiment 3. (a, b) Percentages of correct displacement discriminations for the 'blanking effect' condition. (b) The horizontal and vertical axes represent performance for the 'blank' and 'no blank' conditions, respectively. (c, d) Percentages of target displacement reported for the 'landmark effect' condition. (d) The horizontal and vertical axes represent performance for the 'landmark displacement' and 'target displacement' conditions, respectively. (a, c) Means of all five observers. (b, d) The open circle symbols represent the results of each observer, and the solid square symbols represent the means of all five observers. Error bars represent the standard error of the mean.

mark' and 'target') [$F(1, 4) = 179.27, p < 0.001$], indicating that observers were sensitive to the physical displacement of the target.

To compare the influences of luminance and equiluminance stimuli on the blanking and landmark effects, we replotted the data against color difference on DKL color space (Brainard, 1996; Derrington, Krauskopf, & Lennie, 1984) and CIELAB uniform color space (Fig. 10). Fig. 10a combines the data from the 'blank' and 'no blank' conditions for the blanking effect, and Fig. 10b combines the data from only the landmark displacement condition for the landmark effect. These results show that the effects of stimulus equiluminance are comparable to those of luminance stimuli, with a color difference of about 0.02 for both the blanking and landmark effects.

5. General discussion

This study revealed that luminance contrast has a strong effect on both the blanking effect and the landmark effect. We found that with target blanking, the capability to correctly detect target displacements across saccades profits in a very similar way from an increase of target contrast in both effects. We also found that the contrast of the continuously presented landmark did not influence the landmark effect, indicating that stimulus contrast matters only when the stimulus is blanked. These results suggest that a common process modulates the localization accuracy of a briefly blanked

target for the blanking and landmark effects. We also found that the landmark effect, expressed by the bias λ , is independent of target contrast. The value of λ , which represents the position of the criterion relative to the midpoint between the target and landmark distributions in the SDT analysis, shifts toward the landmark distribution by an approximately constant amount for different target contrasts. Thus, the landmark effect can be expressed as a bias toward the landmark displacement, indicating that relative displacements of target and landmark tend to be perceived as target displacements. Additionally, Experiment 3 showed that the blanking and landmark effects are different under equiluminant conditions. The blanking effect disappeared with equiluminant chromatic stimuli, while a robust landmark effect was still observed. Taken together, these results suggest that the blanking and landmark effects rely on a common process for target displacement detection, and that the landmark effect can be regarded as a bias in the decision criterion. Moreover, the effect of luminance contrast suggests that transient signals after the saccade play an important role in the blanking and landmark effects.

Higgins and Wang (2010) and Deubel, Koch, and Bridgeman (2010) argued that the blanking and landmark effects have different underlying mechanisms. Specifically, the blanking effect is specific to the occurrence of a saccade (Deubel et al., 1996), while the landmark effect has been observed even in the absence of saccades (Deubel et al., 2010; Higgins & Wang, 2010). Moreover, a pre-

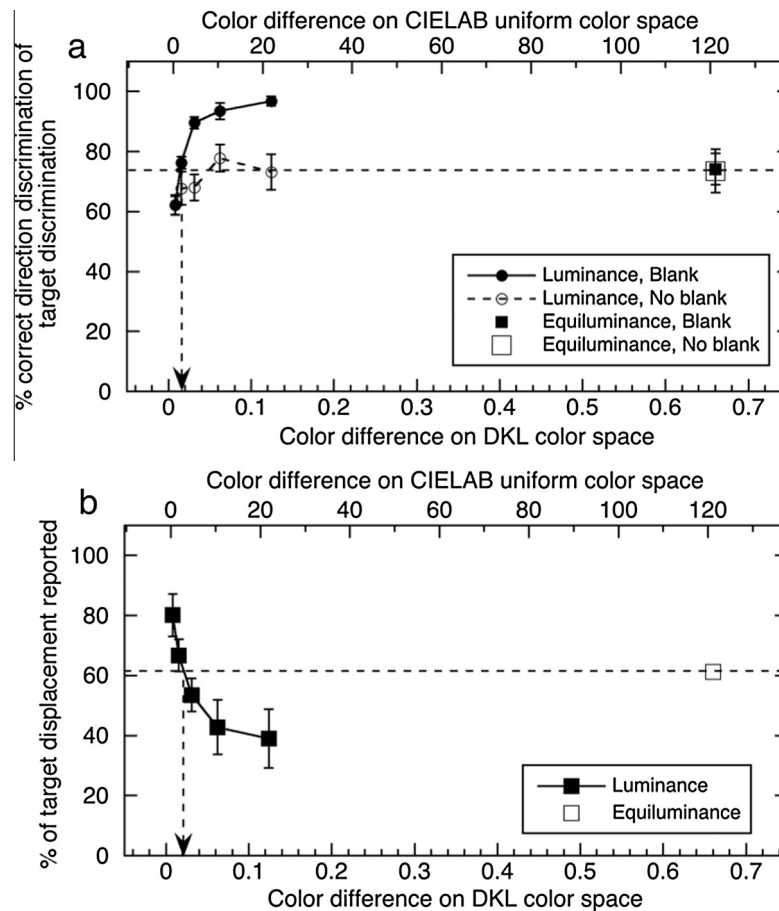


Fig. 10. Comparison of the effects of luminance and equiluminant stimuli on the blanking and landmark effects. (a) Blanking effect. Solid and open symbols represent the blank and no-blank conditions, respectively. The circle and square symbols represent the luminance and equiluminant stimuli, respectively. (b) Landmark effect. Data are from only the landmark displacement condition in Experiments 2 and 3. Solid and open symbols represent the stimuli with luminance contrast and equiluminant stimuli, respectively. The color difference is in either DKL color space (bottom) or Lab color space (top) calculated using the CIE XYZ system. Note that although the Judd-Vos modified version of XYZ is required to calculate the DKL color space, we used the CIE XYZ system here as an approximation because Judd-Vos modification influences red and green to some extent. $N = 5$. Error bars represent the standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vious study suggested that saccadic compression of visual space (Dassonville, Schlag, & Schlag-Rey, 1995; Honda, 1993, 1995, 1999; Lappe, Awater, & Krekelberg, 2000; Matsumiya & Uchikawa, 2001; Ross, Morrone, & Burr, 1997) is related to the landmark effect but not the blanking effect (Matsumiya & Uchikawa, 2003). Indeed, the characteristics of saccadic compression are similar to those of the landmark effect reported in our study. The strength of saccadic compression of visual space is contrast-dependent, with low-contrast stimuli leading to stronger compression than high-contrast stimuli (Michels & Lappe, 2004). In addition, saccadic compression occurs for equiluminant chromatic-modulated stimuli as well as luminance-modulated stimuli (Morrone, Ross, & Burr, 1997; Ross et al., 1997). Our findings suggest that the landmark effect has different mechanisms from the blanking effect on decision bias, although the two effects rely on a common mechanism for target displacement detection. Target localization improves with luminance contrast similarly for both the blanking and landmark effects. So, on one hand, high target contrast supports the improvement resulting from brief blanking of the target in the blanking effect. On the other hand, high target contrast weakens the effect of bias toward response to the landmark displacement in the landmark effect. With a constant bias λ , the smaller d' resulting from a reduction of target luminance contrast increases the false-alarm rate, leading to higher percent-

ages of erroneously perceived target displacement when the landmark is displaced.

We suggest that the difference in bias between the blanking and landmark effects provides a clue to the underlying mechanisms. There are two cues for detecting target displacement during a saccade: extra-retinal information about eye position, and retinal information about the location of the target relative to a landmark (Niemeier, Crawford, & Tweed, 2003, 2007). If there is no landmark around the target, the visual system must rely on extra-retinal information to perceive target displacement across a saccade. However, it has been suggested that the visual system does not use this extra-retinal information when the target is continuously present (Bridgeman et al., 1975; Deubel et al., 1996), perhaps because the visual system makes the assumption that the visual world is stable during saccades (the so-called stable-world assumption). The blanking effect, on the other hand, suggests that the visual system does use extra-retinal information if the target is blanked after a saccade (Deubel et al., 1996). Our finding of a larger blanking effect with higher luminance contrast suggests that transient signals from target reappearance after the saccade interfere with this stable-world assumption.

If there is a landmark around the target, however, the visual system can use the relative location between target and landmark to infer target displacement. In this case, the visual system does not need to use extra-retinal information. In the landmark effect,

the actual displacement of the (continuously present) landmark during a saccade is not perceived because the visual system uses the stable-world assumption; instead, an illusory displacement of the blanked target is perceived due to the change in distance from the landmark. Our results show that the decision criterion is biased toward responding to the landmark displacement, and that this bias is approximately constant across target contrasts. With a constant bias in the decision criterion, the landmark effect decreases with the improvement of target displacement as mentioned above. This suggests that the relative weights of retinal and extra-retinal information may determine the strength of the landmark effect. The contrast dependence of both the blanking effect and the landmark effect can be explained by transient signals arising from post-saccadic target reappearance evoking extra-retinal signals that disrupt the stable-world assumption (Deubel et al., 1996), whether or not a landmark is present.

We found that target contrast influences saccade latency, as reported in a previous study (Ludwig, Gilchrist, & McSorley, 2004). Longer saccade latencies increase the time to preview the target before a saccade. A recent study showed that increased preview time improves the detectability of target displacement during saccades (Zimmermann, Morrone, & Burr, 2013). Therefore, the longer preview times caused by low target contrast may improve the detectability of target displacement in the blanking-effect and landmark-effect experiments. However, in our experiments, the detectability of target displacement was higher with high target contrast than with low target contrast. Moreover, our experiments showed that saccade latency was longer in the no-blank condition than in the blank condition. These results are opposite to those predicted by the preview time.

What are possible mechanisms underlying target localization related to saccades, and thus the blanking and landmark effects? The luminance and chromatic pathways, thought to correspond to the magnocellular and parvocellular pathways involved in the layers of the lateral geniculate nucleus (LGN), are considered functionally separate visual streams from the retina to the cortex (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Livingstone & Hubel, 1988; Meringan & Maunsell, 1993; Schiller & Colby, 1983). Previous studies have argued that saccadic suppression is stronger in the magnocellular pathway than in the parvocellular pathway (Burr et al., 1994; Sato & Uchikawa, 1999; Uchikawa & Sato, 1995). As motion perception is mediated mainly by the magnocellular pathway (Cavanagh, 1987; Livingstone & Hubel, 1988) while color contribution to motion may indicate influence of the parvocellular pathway (Cropper & Wuerger, 2005; Shioiri, Yoshizawa, Ogiya, Matsumiya, & Yaguchi, 2012), suppression of the magnocellular pathway may prevent retinal motion signals elicited by saccades from reaching perceptual systems. Indeed, Shioiri and Cavanagh (1989) showed that low-level motion cannot be detected during saccades, although a previous study reported that the magnocellular pathway functions during saccades if a stimulus is spatiotemporally optimal for motion detection by this pathway (Castet & Masson, 2000). Furthermore, a physiological study investigating the different contrast response properties of parvocellular and magnocellular LGN neurons (Shapley, 1990) demonstrated that neural responses increase much more steeply as a function of contrast for magnocellular neurons than for parvocellular neurons. As this finding is quite similar to our results shown in Fig. 2f, we speculate that the results under the no-blank condition reflect the response of parvocellular neurons, while those under the blank condition reflect the response of magnocellular neurons. Indeed, saccadic suppression occurs strongly under the no-blank condition, in which the magnocellular pathway is selectively suppressed. The parvocellular pathway may therefore become dominant under the no-blank condition. Yet, transient signals after a saccade that are presented only under the blank condition may be able to access

the magnocellular pathway. Thus, our finding that the effect of brief blanking of a target is facilitated by luminance contrast suggests that transient signals from a postsaccadic reappearing blanked target may escape selective suppression of the magnocellular pathway during saccades. This is also consistent with the fact that the contrast of the continuously presented landmark does not influence target localization ability for the landmark effect, because the continuously presented landmark does not produce transient signals. If neural responses in the magnocellular pathway are critical, stimulus contrast matters only when the stimulus is blanked.

In summary, we investigated the modulation of the blanking and landmark effects by stimulus contrast. Our results reveal that target localization ability improves with luminance contrast for both effects similarly, and that the decision criterion is biased toward the landmark displacement if a continuous landmark is present. Further, the blanking effect was not found with equiluminant stimuli, while the landmark effect was. The analysis of these results suggests that the blanking and landmark effects rely on a common luminance-based process in target localization, but have different effects on decision bias. We conclude that luminance-based transient signals make an important contribution to visual stability, and to the relative weight of retinal and extra-retinal information in target localization across saccades.

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