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The role of presaccadic compression of visual space in spatial remapping across saccadic eye movements

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Abstract

When multiple bars are briefly flashed near the saccadic goal on a visual reference just before a saccade, the total width of the multiple bars appears to be compressed toward the saccadic goal. We show that presaccadic compression of visual space is related to the attribution of the displacement of a visual stimulus to the displacement of another stimulus appearing after the saccade. Subjects observed a bar and a ruler. The bar was displaced during a saccade and the ruler disappeared briefly at the same time, and then the ruler reappeared at the same location after the saccade. The subjects had the impression that the bar appeared to remain stationary and the ruler appeared to be displaced after the saccade. This impression occurs strongly when the amount of the compression of visual space reaches the maximum at the saccade onset. Also, it occurs only at the saccadic goal in the same way as presaccadic compression of visual space. Saccadic suppression of displacement was equivalent at the saccadic goal and in the location opposite to the saccadic goal, indicating that the attribution of the bar displacement to the displacement of the ruler appearing after the saccade is not a consequence of saccadic suppression of displacement. Furthermore, performing a direction discrimination task showed that the bar appears stationary at the saccadic goal during compression of visual space even when the bar was actually displaced. We interpret these results as showing that presaccadic compression of visual space establishes the location of the saccadic goal (the bar) as a reference and then the location of the ruler is remapped relative to the reference location after the saccade, resulting in the illusory displacement of the ruler.

Keywords: Saccade; Visual space; Displacement; Remapping; Compression of space; Visual stability

1. Introduction

How does the visual system achieve visual stability during saccadic eye movements? This question has been considered beginning with the work of Helmholtz (1866). Recently, some studies have suggested that 'presaccadic compression of visual space' plays an important role in achieving visual stability. These studies showed that the apparent number of bars in a multiple bar array flashed at the saccadic goal on a visual reference decreases near the time of saccadic onset (Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). The time course of the phenomenon is consistent with the mislocalization of stimuli flashed during saccades (Morrone et al., 1997; Ross et al., 1997). The magnitude of the compression is consistent with the change in width that would be predicted by presaccadic mislocalization (Matsumiya & Uchikawa, 2001). In addition, Lappe, Awater, and Krekelberg (2000) found that presaccadic compression of visual space occurs only when visual references are available just after a saccade, and Deubel, Schneider, and Bridgeman (1996) found that postsaccadic visual information is needed for visual stability during saccades.

How can presaccadic compression of visual space contribute to visual stability? Visual stability requires a remapping process in which the positions in the new retinal image are associated with the previous retinal

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images across a saccade. Presaccadic compression of visual space may be a part of the remapping process in the following way.

Remapping involves a prediction that the internal representation of space shifts into the new coordinates of the next intended fixation (Duhamel, Colby, & Goldberg, 1992). This suggests that presaccadic compression may occur in the predicted, postsaccadic coordinate system. Ross et al. (1997) and Morrone et al. (1997) constructed a model for a presaccadic shift in the same direction and of the same amplitude as the saccade, together with compression of visual space, and found that the shift fit well with the anticipatory behavior of cells in the lateral intraparietal area (LIP) of alert monkeys. In addition, Gottlieb, Kusunoki, and Goldberg (1998) found that cells in the LIP responded to stimuli brought into their receptive field by saccades only when the stimuli had behavioral significance. The results of Ross et al. (1997), Morrone et al. (1997), and Gottlieb et al. (1998) suggest that presaccadic compression of visual space may occur in an internal representation of space where only the most salient or behaviorally relevant objects are represented.

The work reviewed above suggests that only the representation of the saccadic goal, and not other objects, is stable across saccades. In a representation of the space that includes the saccadic goal and other objects, presaccadic compression should occur toward the saccadic goal. If the saccadic goal is displaced just before a saccade, the object may appear to remain stationary because the presaccadic compression of visual space compresses the distance of the displacement in the internal representation of the space. Thus, the presaccadic compression of visual space fixates the location of the object in the internal representation of the space, establishing a reference location. As a result, the locations of the other objects may be remapped relative to the reference location after the saccade.

Consider the following case. A vertical bar and a ruler are presented in a display, as shown in Fig. 1a. An observer makes a saccade toward the bar from a fixation point located at −10 on the ruler. The ruler disappears just before the occurrence of the presaccadic compression of visual space, and the bar is displaced during the presaccadic compression of visual space. After the saccade, the ruler appears at the same location again. The relative positions of the bar and the ruler are different before and after the saccade. If the bar is the reference location for the remapping of visual space, then the bar will appear to have remained stationary and the ruler will appear to have been displaced relative to the location of the bar after the saccade. Deubel, Bridgeman, and Schneider (1998) found that a blanked stimulus appeared to be displaced after a saccade, although in fact a different stimulus had been displaced during the saccade. Therefore, this phenomenon found by Deubel et al. (1998) may be closely related to presaccadic compression of visual space.

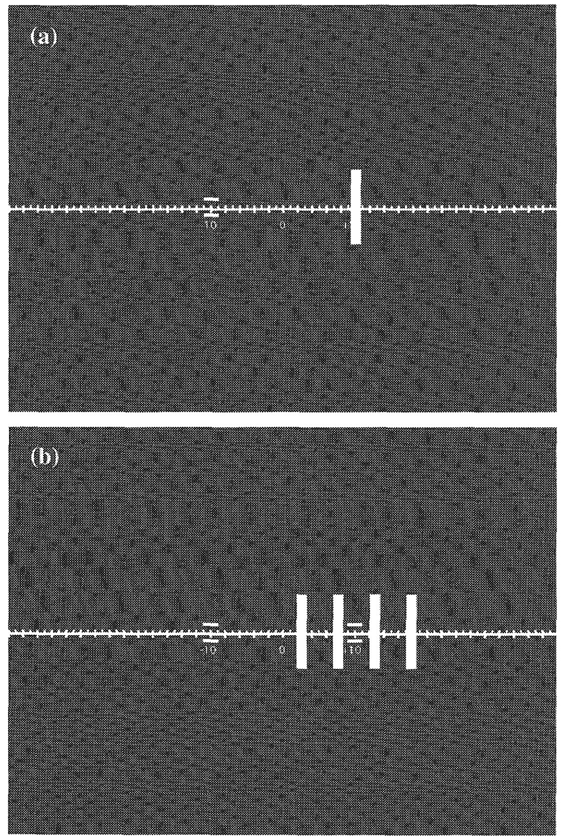


Fig. 1. Arrangement of visual stimuli in experiment 1. (a) The displacement condition; (b) the width condition.

The present study, consisting of four experiments, was conducted to investigate the role of presaccadic compression in the remapping of locations across saccades.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Four subjects whose age ranged from 23 to 30 years old and had normal vision participated in this study. Three of them (HM, HA, and SM) were experienced in other experiments in which their saccadic eye movements were measured, and they were naïve with respect to the purpose of this study. The other subject (KM) was one of the authors. Subjects HM and KM participated in all the experiments. Subject HA participated in experiments 1, 2, and 4. Subject SM participated only in experiment 3.

2.1.2. Apparatus

Subjects sat in the dark for 3 min before starting the experiment. The subject's head was fixed with a combination of a bite bar and a forehead rest. The viewing distance was 25 cm. Visual stimuli were presented on a CRT display with a refresh rate of 75 Hz. The display subtended 59° high and 74° wide, and was controlled by a computer (Apple Macintosh).

A limbus-tracking device, which consisted of two infrared emitting diodes and two photo diodes, was used to measure horizontal eye-movement of the subject's left eye with an accuracy of 0.1°. The signal from the device was recorded by the computer with an A/D converter at a sampling rate of 75 Hz. We differentiated the trajectory of the eye position to obtain the velocity of the eye movement. The onset of a saccade was defined as the time at which eye velocity exceeded 30°/s. This triggered the presentation of the visual stimulus in experiments 1 and 4. Saccadic latency was defined as the period between the onset of target and the onset of saccade.

2.1.3. Calibration of eye-movement

Each trial started with a calibration procedure. In the procedure, the subject fixated five dots presented on a horizontal center line of the display sequentially, and pushed a button after each fixation was completed. Horizontal eye positions expressed as a voltage when the button was pushed and the corresponding dot positions on the screen were recorded by the computer. 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. Two horizontal red rectangles (0.5° in height, 2.0° in width) were presented at −10° horizontally from the display center to act as the fixation cue (Fig. 1a). A saccade cue, which was the same configuration as the fixation cue, was presented at 10° horizontally from the center in addition to the fixation cue (Fig. 1b). The test stimulus consisted of four regularly spaced vertical bars (10° in height, 1.4° in width) that were flashed for 13.3 ms around the location of the saccade cue. The total width of the test stimulus was chosen randomly from values between 15.0° and 11.7°. The delay of test stimulus presentation from saccade onset was varied randomly from trial to trial. The reference stimulus, also consisting of four bars (total width = 13.5°), was presented following the presentation of the test stimulus (see *Procedures* for the details).

The luminances of the stimulus items mentioned above and the background were 15 and 2.0 cd/m^2, respectively. Beside the ruler, the monitor frame could serve as another visual reference. However, the monitor frame was very eccentric (it subtended 59° high by 74° wide).

2.1.5. Procedures

Two kinds of trials were tested, displacement and width.

Fig. 2a shows an example of the sequence for a displacement trial. The subject fixated the fixation cue and pressed a button to start the trial. After a delay selected randomly to be between 500 and 1000 ms, the fixation cue was extinguished and a bar stimulus appeared at the division of +10 on the ruler. Then, the subject made a 20° rightward saccade towards the bar as soon as possible. The ruler was extinguished 50 ms after the onset of the bar. The bar remained visible until all stimuli were extinguished at the end of the trial. Either the bar or the ruler was displaced 0.3° to the left or right between −100 and +100 ms relative to the saccade onset. The timing of the displacement occurring before saccades was selected based on the averaged saccade onset over the past four trials. This averaged saccade onset was used only to present the intended stimulus condition efficiently. For data analysis, actual saccade onset was used to specify the timing of bar displacement relative to the saccade. The timing of displacements after saccades was based on the actual saccade onset. The ruler was presented again 110 ms after the actual saccade onset. If the bar was displaced, the ruler reappeared at the same position as before the ruler was extinguished. If the bar remained stationary, the ruler reappeared at the displaced position. All stimuli were extinguished 200 ms after the ruler reappeared. The subject reported whether the bar or the ruler was displaced. Each subject performed 5 sessions and each session consisted of 60 trials of the bar displacement conditions and 60 trials of the ruler displacement conditions.

Fig. 2b shows an example of the sequence of stimulus presentations in the width measurement trials. The stimulus sequence was basically the same as the displacement trials except for the following. The saccade cue was presented after the fixation cue was extinguished. A random time later, a four-bar test stimulus was presented for 13.3 ms around the saccade cue. The timing of the four-bar stimulus presentation was decided in the same way as the timing of bar displacement in the displacement measurement, described above. The total width of the four-bar stimulus was randomly selected to be either 15.0° (large) or 11.7° (small). The ruler reappeared 110 ms after the actual saccadic onset. All stimuli were extinguished 200 ms after the ruler reappeared. Following the sequence of the test stimulus presentation in Fig. 2b, the reference stimulus was presented in the following way. The fixation cue and the ruler were presented in the display again 200 ms after the disappearance of all the stimuli. The subject fixated the fixation cue and pressed a button to continue the trial. Although the saccade cue was presented after the fixation cue was extinguished, the subject did not make any saccades. The reference stimulus, consisting of four bars

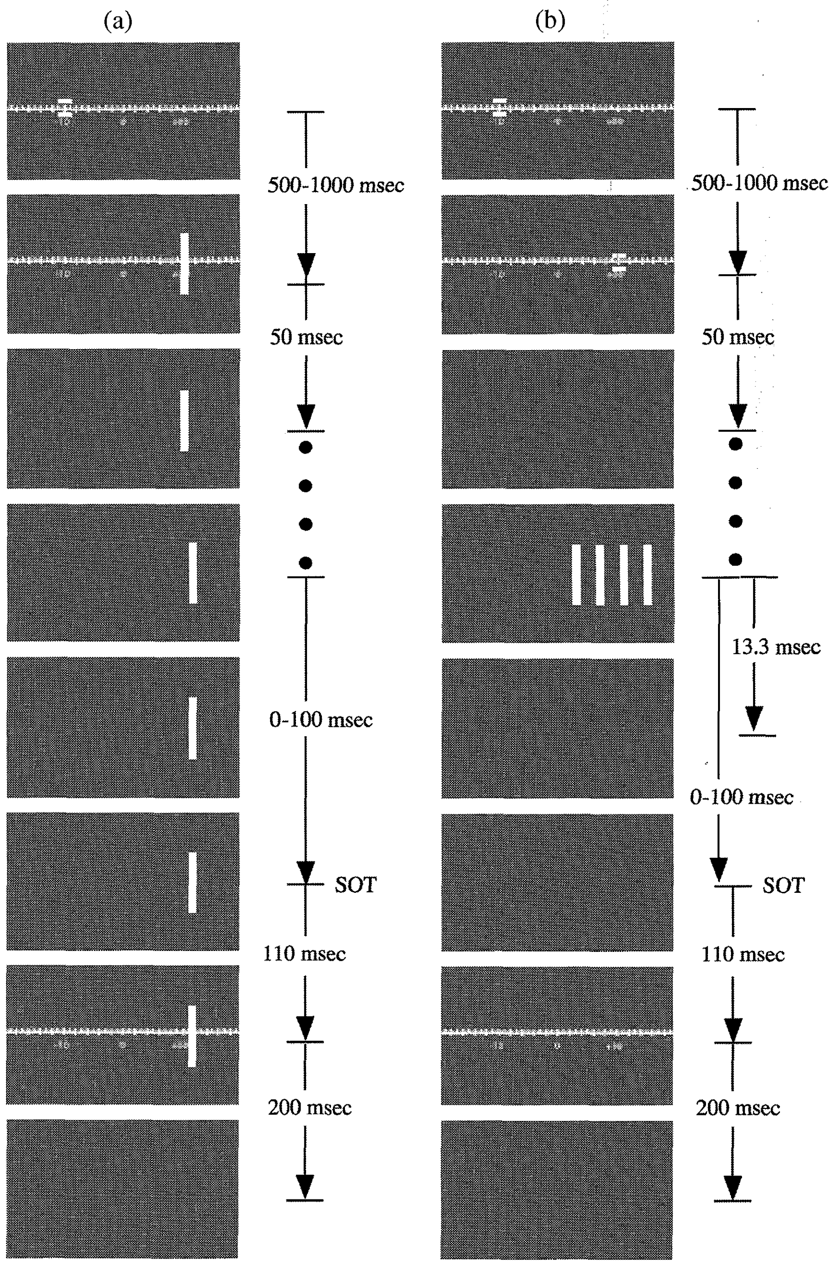


Fig. 2. Stimulus sequence in experiment 1. (a) Displacement measurement; first, a subject fixated the division of −10, then pressed a button. After a waiting period of 500–1000 ms, a visual cue at the division of −10 was extinguished and a bar appeared at the division of +10. The subject made a saccade toward the bar as quickly as possible. 50 ms after the appearance of the bar, the ruler was extinguished. After a randomly delay of −100 to +100 ms relative to the saccade onset time (SOT), the bar was displaced 0.3° to left or right in the period of 13.3 ms, or the bar remained stationary. In this sequence, the delay from the saccade onset is selected from between −100 and 0 ms, and the bar was displaced to right. 110 ms after the actual saccade onset, the ruler appeared again. After a delay of 200 ms, all stimuli were extinguished. (b) Width measurement; the sequence is the same as mentioned above except that a four-bar stimulus was flashed for 13.3 ms around the saccadic goal.

(see *Stimuli* for the details), was presented for 13.3 ms around the saccade cue, 26.7 ms after the saccade cue and the ruler were extinguished. The ruler reappeared 110 ms after the disappearance of the reference stimulus. All stimuli were extinguished 200 ms after the ruler reappeared. Finally, the subject reported which was wider, the four-bars in the presaccadic test trials or the four-bars in the reference stimulus presented during fixation. Each subject performed 6 sessions and each session consisted of 120. In 90 and 30 trials of them, the test stimuli were larger and smaller than the reference stimulus, respectively.

2.2. Results and discussion

First, we measured the time course of the detection of the bar displacement around saccades. Fig. 5a shows the percentages of correct detections of bar displacements as

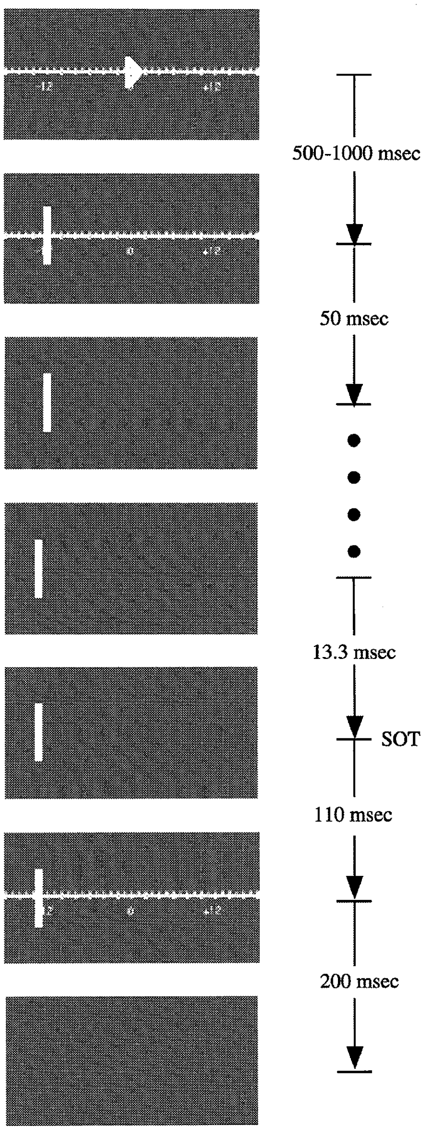


Fig. 3. Stimulus sequence in experiment 2. First, a subject fixated a triangle which indicated the saccade direction, and then pressed a button. After a waiting period of 500–1000 ms, the triangle disappeared and a bar appeared at the division of −12 or +12. Each division served as a saccade target. The direction of the triangle decides which of their divisions is the saccade target. The subject made a saccade toward the saccade target after the triangle disappeared. 50 ms after the appearance of the bar, the ruler was extinguished. 13.3 ms before the predicted saccade onset time (SOT), the bar was displaced 0.3° to left or right in the period of 13.3 ms, or the bar remained stationary. 110 ms after the actual saccade onset, the ruler appeared again. In this sequence, the bar appeared at the division of −12 and was displaced to left. After a delay of 200 ms, all stimuli were extinguished.

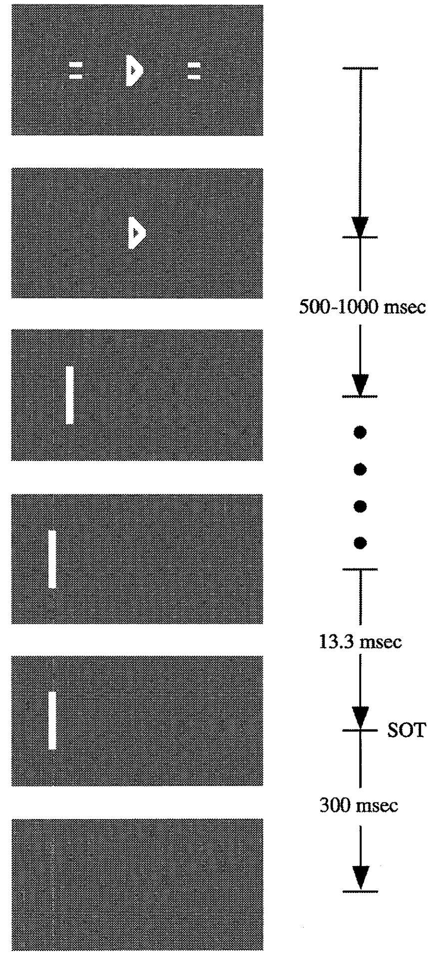


Fig. 4. Stimulus sequence in experiment 3. First, a triangle and two saccade cues were presented in the display. A subject fixated the triangle indicating a saccade direction while remembering the locations of the two saccade cues. After the subject pressed a button, the saccade cues were extinguished. The subject pressed another button. After a waiting period of 500–1000 ms, the triangle was extinguished and a bar appeared on the left or right side in the display. Either of the two saccade cues represented the location of the saccade target. The subject made a saccade toward the target after the triangle disappeared. 13.3 ms before the predicted saccade onset time (SOT), the bar was displaced 0.3° to left or right in the period of 13.3 ms, or the bar remained stationary. In this sequence, the bar appeared on the left side and was displaced to left. After a delay of 300 ms, all stimuli were extinguished.

a function of time relative to the saccade onset, and shows the results when the bar was actually displaced and the ruler remained stationary. Detection declined when the bar was displaced −30 to 80 ms relative to the saccade onset. Detection performance of 0% for the bar displacement means that the subject perceived the illusory displacement of the ruler. The illusory displacement of the ruler is consistent with the blanking effect found by Deubel et al. (1998). When the ruler was displaced and the bar remained stationary in the display, the percentages of correct responses for the ruler displacement for subjects HM, KM, and HA were 80.9%, 96.3%, and 72.5%, respectively.

Second, we measured the time course of the width compression of a four-bar stimulus around saccades. Fig. 5b and c show the percentages of the "large" reports for the large stimulus and those for the small stimulus as a function of time relative to the saccade onset, respectively. In Fig. 5b, the "large" responses for large-width test stimulus decreased within the range of −50 and 75 ms relative to the saccade onset for subjects

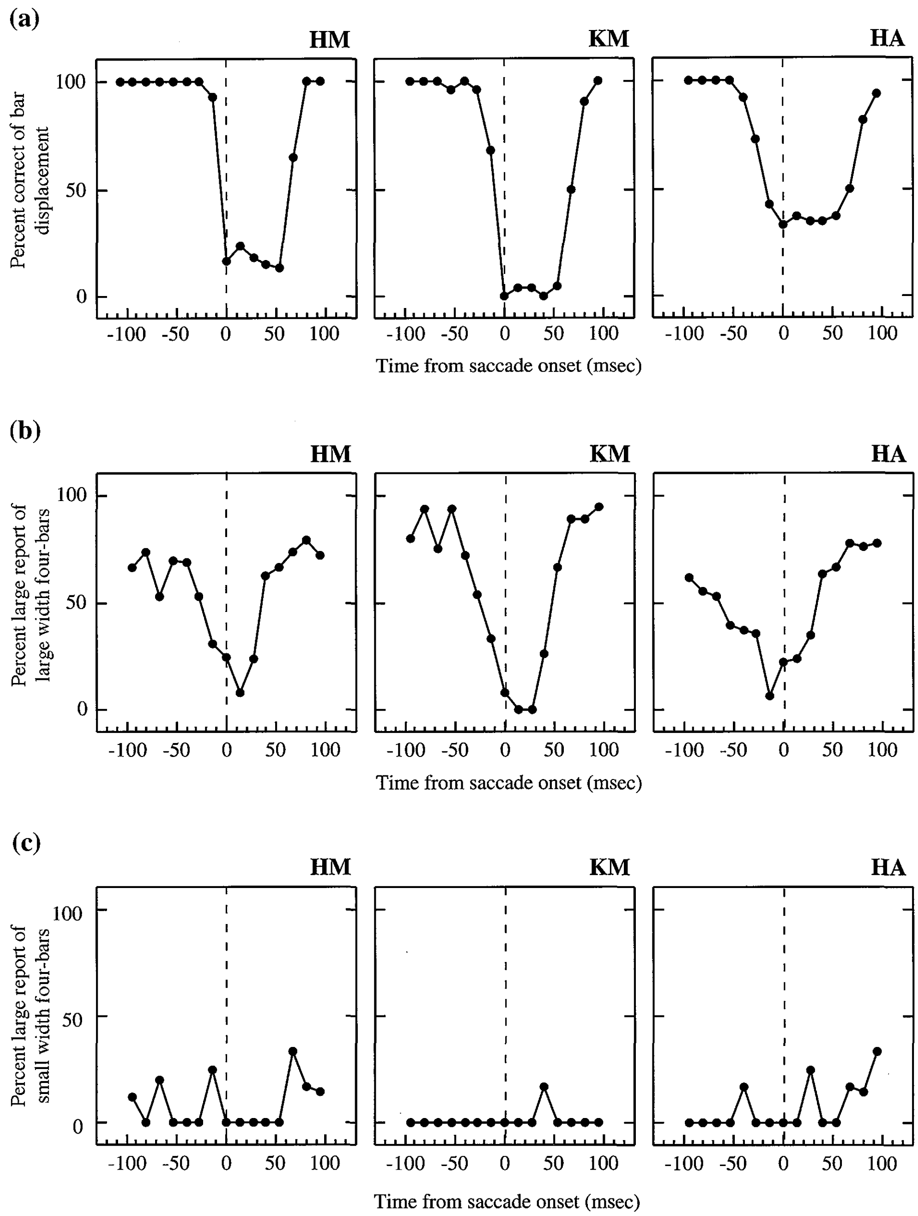


Fig. 5. Results of experiment 1. (a) Percent correct detection of bar displacement as a function of time relative to the saccade onset. (b,c) Percent reporting to be larger than the width of the reference stimulus as a function of time relative to the saccade onset. (b) and (c) indicate large and small widths, respectively.

HM and KM. For subject HA, the critical range was from −100 to 75 ms relative to the saccade onset. Thus, the apparent width of the test stimulus was strongly compressed near the saccade onset for all subjects. In Fig. 5c, the "large" response with the small-width test stimulus tended to be constant over the time relative to the saccade onset, indicating that the subjects accurately perceived the apparent width of the test stimulus as small when the width of the test stimulus was smaller than that of the reference stimulus. The results of the apparent width of the four-bar stimulus agreed with those obtained by Ross et al. (1997), Morrone et al. (1997), and Matsumiya and Uchikawa (2001).

A comparison between Fig. 5a and b shows that the width compression of the four-bar stimulus began 30 ms before the detection performance of the bar displacement decreased. Detection of the bar displacement tended to decrease suddenly, while the width compression of the four-bar stimulus reached the maximum around the saccade onset. Why is the timing different between the width and bar-displacement judgements? If the perception of the bar displacement is taken from the internal representation of space compressed by presaccadic compression, then the detectability of the bar displacement should depend on how compressed the internal representation of space is. Fig. 6 shows a pos-

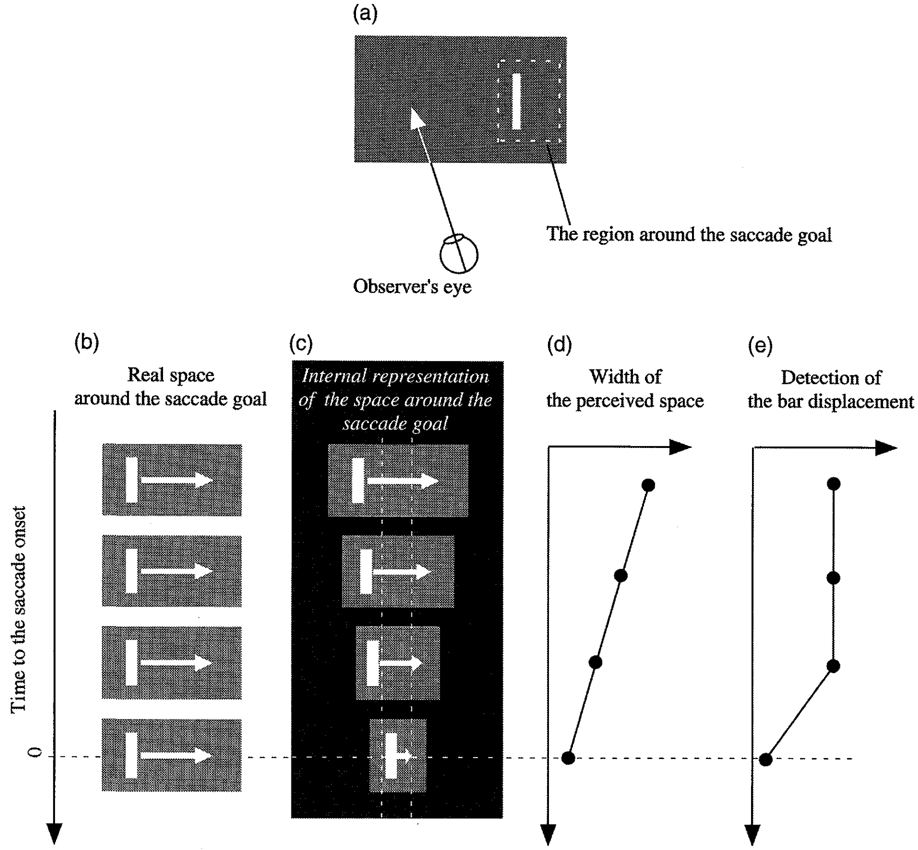


Fig. 6. Concept of the timing difference between the width and bar-displacement judgements. (a) Illustration of the situation that an observer's eye is about to move toward the vertical bar. The dotted rectangle represents the region around the saccadic goal. (b) Real space around the saccadic goal. The gray rectangles correspond to the dotted rectangle in Fig. 6a, representing the width of the space around the saccadic goal. The horizontal arrows show the direction and amplitude of the vertical bar displaced. The width of the space and the amplitude of the bar displacement are constant at any time. (c) Internal representation of the space around the saccadic goal. The gray rectangles and the horizontal arrows are the same as Fig. 6b. The width between the two vertical dotted lines represent the minimum displacement amplitude needed for the detection of the bar displacement. In the internal representation of the space, the width of the space and the amplitude of the bar displacement change depending on the time to the saccade onset. (d) Width of the perceived space as a function of time to the saccade onset. The width of the perceived space decreases as the time to the saccade onset decreases. (e) Detection performance of the bar displacement as a function of time to the saccade onset. The bar displacement is perceived from the internal representation of the space. The detection performance of the bar displacement suddenly declines if the perceived amplitude of the bar displacement does not exceed the minimum displacement amplitude depicted in Fig. 6c.

sible explanation of why the timing is different between the width and bar-displacement judgements. Fig. 6a shows the observer's eye about to move toward the vertical bar. Fig. 6b and c represent the real space and the internal representation of the space around the saccadic goal, respectively. In these figures, the gray rectangles represent the width of the space around the saccadic goal, and the horizontal white arrows represent the direction and amplitude of the vertical white bar displacement. The physical amplitude of the bar displacement is constant whenever the bar is displaced, as shown in Fig. 6b. The perceived amplitude of the bar displacement, however, changes depending on time to the saccade onset, as shown in Fig. 6c. This is because the width of the space gradually decreases as time to the saccade onset decreases in the internal representation of the space. The two vertical white dotted lines depicted in Fig. 6c represent the minimum displacement amplitude needed for the detection of the bar displacement. Thus, width compression can begin before the detection performance of the bar displacement decreases (Fig. 6d and e). These results suggest that *presaccadic* compression of visual space may be closely related to the bar displacement being inappropriately attributed to the displacement of the ruler appearing after the saccade. However, the question arises whether the attribution of the bar displacement to the displacement of the ruler appearing after the saccade is caused by presaccadic compression of visual space or by saccadic suppression of displacement. Experiments 2 and 3 demonstrate that the attribution of the bar displacement to the ruler displacement is due to presaccadic compression of visual space.

A comparison of Fig. 5a and b also shows that the minimum detection performance of the bar displacement was maintained for 50 ms from the saccade onset even though the apparent width of the four-bar stimulus began to increase from the maximum of the width compression, suggesting that the width compression of the four-bar stimulus is not related to the decrease of the detection performance of the bar displacement *after* the saccade onset. This is possibly because the location of the bar is kept in a visual memory just before a saccade and the visual system uses the positional information of the bar registered with the visual memory for the remapping during the saccade.

3. Experiment 2

Experiment 2 examined whether the attribution of the displacement of a visual target to the displacement of another stimulus, appearing after the saccade, occurs at the saccadic goal distinctively. Presaccadic compression of visual space occurs at the saccadic goal. If the perceived displacement of the visual target is related to the presaccadic compression of visual space, then one would predict that the perceived displacement of the visual target will be strongly reduced at the saccadic goal.

In experiment 2, we compared detection of bar displacement just before saccades at the saccadic goal with the location opposite to the saccadic goal. If the attribution of the bar displacement to the displacement of the ruler appearing after the saccade is caused by presaccadic compression of visual space, then the detection of the bar displacement should decrease largely at the saccadic goal as compared with the location opposite to the saccadic goal. This is because presaccadic compression of visual space occurs at the saccadic goal. Experiment 2 confirms that the attribution of the bar displacement to the ruler displacement occurs at the saccadic goal in the same way as presaccadic compression of visual space.

3.1. Methods

In experiment 2, the fixation cue was a red arrow at the display center (1.6° in height, 1.6° in width) whose direction indicated the saccade direction (Fig. 3). A horizontal ruler was also presented, with divisions at −12° and +12° from the display center. These divisions were the saccadic targets.

Fig. 3 shows an example of the sequence for a single trial. The subject fixated the center of the arrow presented at the display center and started the trial with a button press. After a random delay (500–1000 ms), the arrow was extinguished and the bar stimulus was presented at either −12° or +12° (randomly selected) from the display center. The subject made a 12° horizontal saccade towards either the −12° (left) or +12° (right) division of the ruler in the direction indicated by the arrow. The ruler was extinguished 50 ms after the onset of the bar. The bar remained visible until all stimuli were extinguished in a trial. At a random time, the bar or the ruler was displaced 0.3° to the left or to the right. The bar displacement was 13.3 ms before the averaged saccade onset over past four trials. This averaged saccade onset was used only to present the intended stimulus condition efficiently. For data analysis, actual saccade onset was used to specify the timing of bar displacement relative to the saccade. Trials were excluded from the data analysis if the bar was not displaced between −30 and 0 ms relative to the actual saccade onset in each trial. The ruler was presented again 110 ms after the actual saccade onset. If the bar was displaced, the ruler reappeared at the same position as before the ruler was extinguished and if the bar remained stationary, the ruler reappeared at the displaced position. All stimuli were extinguished 200 ms after the ruler was presented again. The subject reported whether the bar or the ruler was displaced. Each subject performed 5 sessions and each session consisted of 96 trials.

In control trials, the same sequence of visual stimuli described above was presented while the subject maintained fixation at the display center. Each subject performed 96 trials. Trials containing saccades were cancelled and repeated at another time during the session.

3.2. Results and discussion

Fig. 7 shows the percentages of correct detection of the bar displacement as a function of time relative to the saccade onset. The solid and open symbols represent the detection performances of the bar presented in the same and opposite sides of visual field relative to the saccade direction, respectively. Fig. 8 shows the mean percentages of correct detections of the bar displacement (Fig. 8a) and ruler displacement (Fig. 8b) obtained between −26.66 and 0.0 ms relative to the saccade onset. In Figs. 7 and 8a, the detection of the bar displacement decreased largely in the direction of the saccade compared with the opposite side. Fig. 8b, however, shows that detection of the ruler displacement was not different for the two visual fields, indicating that the subjects could detect the actual displacement of the ruler at a high rate in either the same or opposite side of visual field relative to the saccade direction.

By comparison between Fig. 8a and b, the percentages of correct detection of the bar displacement in the opposite direction of the saccade were similar to that of the ruler displacement. ANOVA with repeated-measures on the percent correct with session, direction (same vs. opposite), and stimulus (bar vs. ruler) confirmed these results. The interaction between direction and stimulus was significant ($P < 0.05$). The main effect of the direction was significant ($P < 0.05$). The main effect of the stimulus was not significant. These results indicate that the attribution of the bar displacement just before a

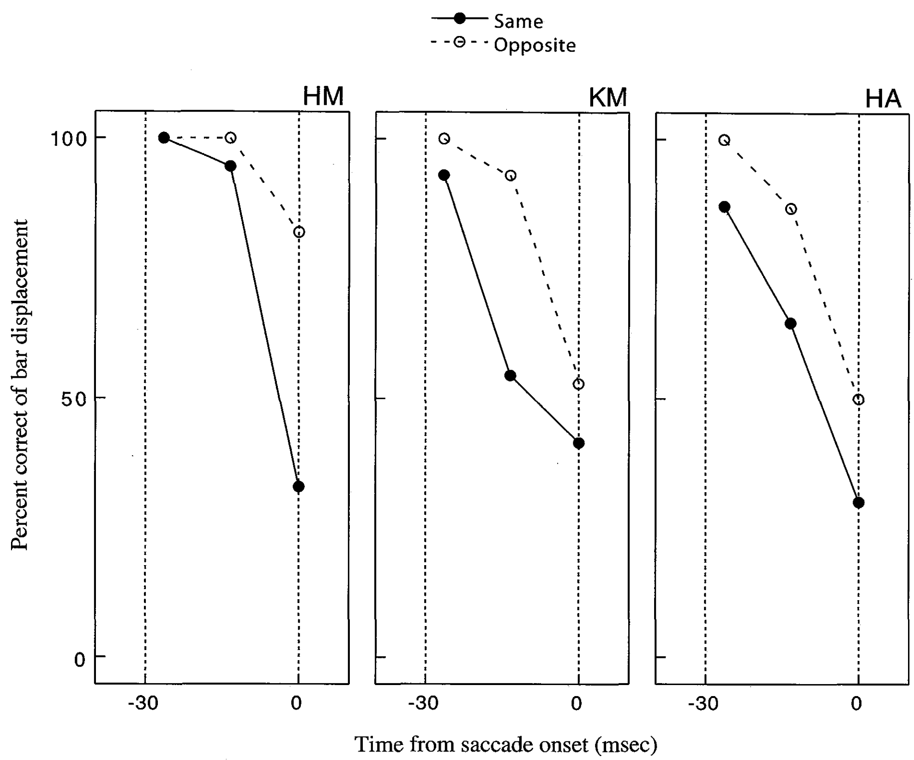


Fig. 7. Percent correct detection of bar displacement as a function of time relative to the saccade onset in experiment 2. The solid and open symbols represent a bar presented in the same and opposite sides of visual field relative to the saccade direction, respectively. The numbers of observations ranged between 11 and 63.

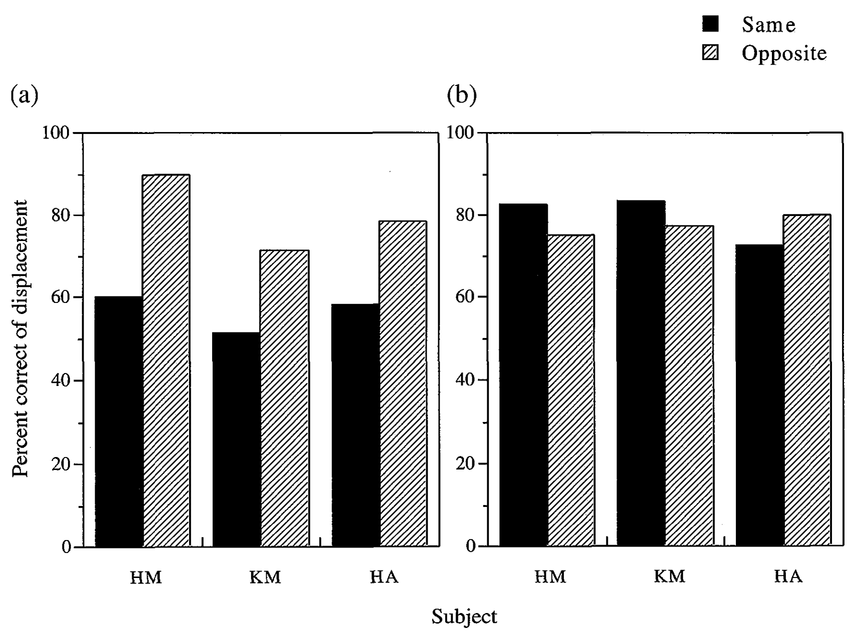


Fig. 8. Results of experiment 2. (a) Percent correct detection of bar displacement for three subjects. (b) Percent correct detection of ruler displacement for three subjects. Solid bars represent a bar presented in the same direction as saccades. Slash bars represent a bar presented in the direction opposite to saccades.

saccade to the displacement of the ruler appearing after the saccade occurs at the saccadic goal in the same way as presaccadic compression of visual space.

In the fixation condition, detection of the bar and ruler displacements in the left and right visual fields were 100% for three subjects. Therefore, a comparison between the saccade and fixation conditions suggests that the perceived displacements of the bar and the ruler were also affected by saccadic suppression of displacement.

4. Experiment 3

Experiment 3 compared saccadic suppression of displacement at the saccadic goal with displacement opposite to the saccadic goal. The saccadic goal and the location opposite to the saccadic goal were equidistant from the fixation point. If the large decrease of the perceived displacement of the bar at the saccadic goal found in experiment 2 was caused by saccadic suppression of displacement, detection of the displacement just before saccades should decrease largely at the saccadic goal as compared with the location opposite to the saccadic goal.

4.1. Methods

Stimuli were the same as experiment 2. Fig. 4 shows an example of the sequence of frames in a single trial. First, the arrow and the two saccade cues were presented at the center of the display. After the subject fixated the arrow and pressed a button to start the trial, the two saccade cues were extinguished. The subject was instructed to remember the positions of the two saccade cues. 500 ms after the subject pressed the button, a beep sounded to signal the subject to press another button. Then, the bar was presented and underwent a random displacement, the same as in experiment 2. The bar was displaced in either of two temporal intervals. The subject reported which interval contained the displacement. Each subject performed 5 sessions consisting of 48 trials each. Trials were excluded from the data analysis if the bar was not displaced between −30 and 0 ms relative to the actual saccade onset in each trial.

In control trials ($n = 48$), the same sequence of visual stimuli described above was presented while the subject maintained fixation at the display center. When a saccade occurred in a control trial, the trial was cancelled and repeated at another time during the session.

4.2. Results and discussion

Fig. 9 shows the percentage of correct detection of the bar displacement in the same and opposite fields relative to the saccade direction. The difference in performance between the same and opposite visual fields was not significant ($t_4 = 1.60$, $P > 0.05$) for three subjects, although bar displacement tended to be detected slightly less accurately in the visual field containing the saccadic goal. Performance in the fixation condition was perfect.

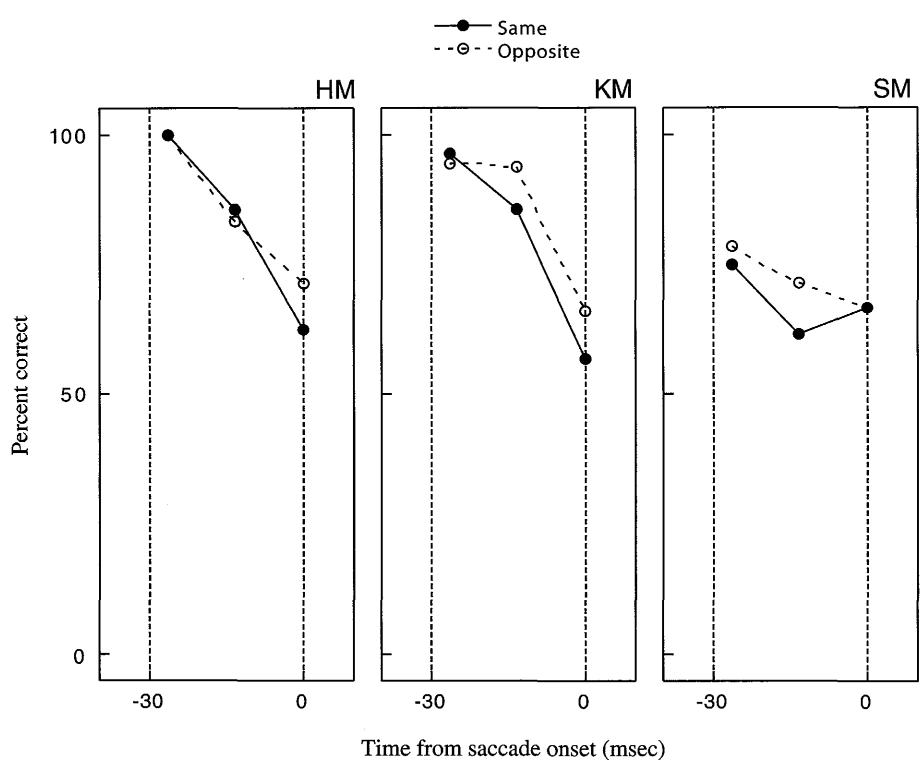


Fig. 9. Percent correct detection of bar displacement as a function of time relative to the saccade onset in experiment 3. Solid and open symbols represent a bar presented in the same and opposite sides of visual field relative to the saccade direction, respectively. The numbers of observations ranged between 7 and 50.

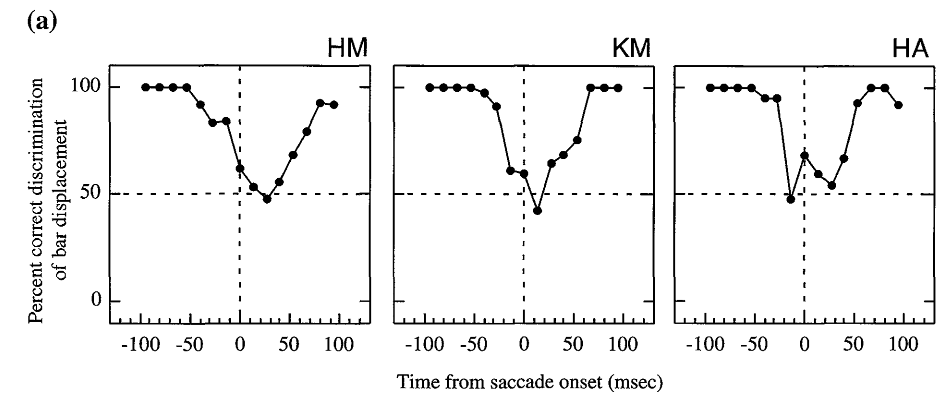
These results show that saccadic suppression of displacement at the saccadic goal is equivalent to that opposite to the saccadic goal. This uniform property of saccadic suppression over the visual field is different from the results in experiment 2, in which the large decrease of the perceived displacement of the bar was found *only* at the saccadic goal.

5. Experiment 4

Experiment 4 examined how the direction of the displacement of the visual target is perceived at the saccadic goal. If the bar appears to be displaced in the opposite direction to the actual displacement of the bar at the saccadic goal during the compression of visual space, this would lead to incongruence between the apparent motion of the bar and the perceived change in the relative position of the bar and the ruler across the saccade. As a result, the subjects may resolve the apparent conflict by attributing all the displacements to the ruler after the saccade. However, if the bar appears stationary at the saccadic goal during compression of visual space, this would lead to the interpretation that the location of the bar is perceptually fixed by presaccadic compression of visual space and then the location of the ruler would be remapped relative to the location of the bar after the saccade. As a result, the subjects may perceive the illusory displacement of the ruler. To decide between these two possibilities, we tested direction discrimination of bar displacement. If the bar appears to be displaced in the opposite direction to the actual displacement of the bar at the saccadic goal in a critical period, then the performance of the direction discrimination for the bar displacement should reach 0%. However, if the bar appears stationary at the saccadic goal in a critical period, then the performance of the direction discrimination for the bar displacement should reach 50%.

5.1. Methods

In experiment 4, the stimulus sequence was basically the same as the displacement measurement in experiment 1 (Fig. 1a), except that subjects performed the direction discrimination of bar displacement, and either the bar or the ruler or both were displaced. If both the bar and the ruler were displaced, the bar was displaced 0.3° to the left or the right, and the ruler was displaced 0.6° in the same direction as the bar displacement. In this case, the direction of the bar displacement was inconsistent with the change in the relative position



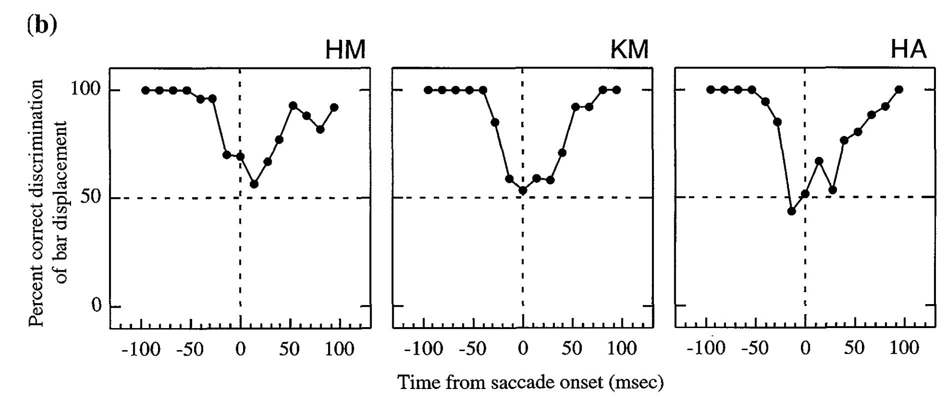


Fig. 10. Results of experiment 4. Percent correct direction discrimination of bar displacement as a function of time relative to the saccade onset. (a) Bar displacement without ruler displacement; (b) bar displacement with ruler displacement.

between the bar and the ruler across the saccade. Thus, subjects could not use the change in the relative position between the bar and the ruler across the saccade for the direction discrimination of bar displacement. In the half of the trials, the bar was displaced and the ruler remained stationary. The subject's task was to report whether the bar was displaced to the left or to the right. Each subject performed 6 sessions consisting of 120 trials each.

5.2. Results and discussion

Fig. 10a shows the percentages of correct discriminations of bar displacements as a function of time relative to the saccade onset under the conditions with "no ruler displacement". In Fig. 10a, the percentages of correct discriminations of bar displacements decreased when the bar was displaced within the range of −50 to 75 ms relative to the saccade onset. The percentages of correct discriminations of bar displacements reached 50% near the saccade onset, indicating that the bar appeared stationary at the saccadic goal near the saccade onset. In fact, the subjects had the impression that the bar sometimes appeared stationary in the trials though the bar was actually displaced in the display.

Fig. 10b shows the percentages of correct discriminations of bar displacements as a function of time relative to the saccade onset under the conditions with "ruler displacement". In Fig. 10b, the percentages of correct discriminations of bar displacements had the same tendency as those in Fig. 10a, indicating that the subjects discriminated the direction of the bar displacement without using the change in the relative position of the bar and the ruler across the saccade.

These results suggest that the bar appears stationary at the saccadic goal when compression of visual space reaches the maximum at the saccade onset. Thus, this leads to the interpretation that the location of the bar is perceptually fixed by presaccadic compression of visual space and then the location of the ruler is remapped relative to the location of the bar after the saccade.

6. General discussion

The present study investigated the role of presaccadic compression of visual space on postsaccadic spatial remapping. We found that the displacement of the bar at the saccadic goal is attributed to the displacement of the ruler appearing after the saccade, indicating that the perceived displacement is transferred from the bar to the ruler. This phenomenon is consistent with the blanking effect found by Deubel et al. (1998). We examined the relation between the attribution of the bar displacement to the ruler displacement and compression of visual space during saccades. Experiment 1 showed the following things. First, compression of visual space temporally precedes the attribution of the bar displacement to the ruler displacement. Second, the attribution of the bar displacement to the ruler displacement was most frequent when compression of visual space reached the maximum at the saccade onset. Experiment 2 showed that the attribution of the bar displacement to the ruler displacement occurs at the saccadic goal in the same way as presaccadic compression of visual space. Experiment 3 showed that the effect of saccadic suppression of displacement is constant at the two eccentricities in the direction and against the direction of the saccade, indicating that the attribution of the bar displacement to the ruler displacement is not a consequence of saccadic suppression of displacement. Experiment 4 showed that the bar appears stationary at the saccadic goal when compression of visual space reaches the maximum at the saccade onset, although the bar was actually displaced. These findings reveal that the location of the bar is perceptually fixed by presaccadic compression of visual space and then the location of the ruler is remapped relative to the location of the bar after the saccade, resulting in the illusory displacement of the ruler. This suggests that presaccadic compression of visual space establishes the location of the bar as a reference location for the remapping of the location of the ruler after the saccade, leading to the conclusion that the role of presaccadic compression of visual space is to establish a reference location for postsaccadic spatial remapping.

In addition, we considered whether the attribution of the bar displacement to the ruler displacement can be explained by the shift of visual attention to the saccadic goal (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986). If the shift of visual attention affected the perceived displacement of the bar in experiment 2, a selective facilitation of the perceived displacement of the bar would have occurred at the saccadic goal. As shown in experiment 2, however, the perceived displacement of the bar was not facilitated but inhibited at the saccadic goal and then the ruler appearing after the saccade was displaced perceptually. This suggests that the results of experiment 2 cannot be explained by the shift of visual attention to the saccadic goal.

The present study provides evidence that an object around the saccadic goal rather than a continuously visible object has an important role in postsaccadic spatial remapping. Deubel et al. (1998) argued that a continuously visible object is perceived as stable and the object becomes the reference for the postsaccadic remapping, even though the object is not the saccade target. If their argument were true, then the results of experiment 2 would have shown that the attribution of the bar displacement to the ruler displacement occurs to the same degree at both of the saccadic goal and the location opposite to the saccadic goal. This is because the bar served as a continuously visible object in both cases. In experiment 2, however, the bar was not perceived as stable when the bar was continuously presented at the location opposite to the saccadic goal. This finding demonstrates that, in addition to the temporal continuity of an object, a continuously visible object needs to exist around the saccadic goal at which presaccadic compression of visual space occurs, in order to become the reference for postsaccadic spatial remapping.

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