Immediate post-saccadic information mediates space constancy

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Abstract

We recently demonstrated that the perceived stability of a visual target that is displaced during a saccade critically depends on whether the target is present immediately when the saccade ends; blanking a target during and just after a saccade makes its intra-saccadic displacement more visible (Deubel et al. Vis Res 1996;36:985–996). Here, we investigate the interaction of visual context and blanking. Subjects saw a saccade target and an equal-sized distractor. During a saccade one or the other was displaced left or right. At the same time, one of the objects could be blanked briefly. Subjects reported whether the target or the distractor had jumped. The object that was blanked was more often seen as jumping (Experiment 1), regardless of which object really jumped, implying that continuously visible objects are preferentially perceived as stable. When both objects were blanked, longer blanking led to better accuracy at identifying which had jumped during a saccade. When one object was jumped and the other, stationary object was blanked (Experiment 2), the blanked object was mistakenly seen as jumping until the jump covered 50% or more of the saccade amplitude. In Experiment 3 a large continuously present texture underwent an undetected jump during a saccade, biasing judgments of simultaneous jumps of a blanked target. The results demonstrate that space constancy in normal situations is dominated by the assumption that a continuously present pattern is stable—this pattern becomes the spatial reference for the post-saccadic recalibration of perceptual space. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Space constancy, limited here to maintaining apparent stability of the visual world despite saccadic eye movements, is normally perfect—the world does not appear to jump in the slightest when the eye moves. The earliest attempts to account for space constancy were cancellation theories, in which the sensory effects of an eye movement are compensated by a simultaneous, equal and opposite extraretinal signal about the position of the eyes in the orbit. The retinal and extraretinal signals cancel each other somewhere in the brain, resulting in a space-constant representation of visual space. In these theories an oculomotor efference copy, proprioception, or some combination of both subtracts from the disturbing effects of a displaced retinal image following a saccade [2].

Cancellation theories cannot support space constancy unaided, however, because the extraretinal signals are not exact copies of the actual eye movement. Their gain (ratio of extraretinal signal to actual eye movement) is usually less than one [3], so they are too small to afford complete compensation. And the gain also depends on other parameters such as oculomotor dynamics [4]. Even a small error would result in a disturbance of constancy.

One compelling solution to this problem is that the visual system has the built-in assumption that the world as a whole does not change during an eye movement. The large background region of the optic array (as opposed to smaller foreground objects) usually does not move in the real world. A visual system that took advantage of this fact would simply ignore all displacements of the optic array as a whole, assigning them instead to movements of the eye. In this case the

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solution to the problem of why the world does not seem to move during an eye movement would be simple: 'Why should it move? The movement of the eye and its retina is registered instead; The retina is proprioceptive' [5]. Unfortunately this simple and powerful idea is easily disproved: a tap on the side of the eye results in apparent movement of the entire optic array, background and all; further, a large afterimage, viewed in darkness, also seems to jump with each saccade [6]. So a more subtle solution must be sought.

An important component of space constancy is saccadic suppression of image displacement (SSID). SSID is an increase in the threshold for detecting a target displacement that takes place during or near a saccadic eye movement. Subjects fail to detect a substantial displacement of a continuously visible image, if the displacement takes place around the time of a saccade [7,8]. Obviously, visual information about object motion that normally would enable detection of the jump at low threshold is severely degraded during a saccade. Without this direct evidence for a target jump, detection of intra-saccadic image displacement requires the comparison of pre- and post-saccadic target locations; SSID implies either that such trans-saccadic information about the location of objects is not available to the visual system, or that the required precise comparison is normally not carried out. It has been suggested that SSID provides an important function in the maintenance of visual stability: it may bridge the errors that occur when imprecise extraretinal signals and retinal input are combined for spatial localizations [9].

SSID seems to imply that precise spatial information about the location of objects is not available across the saccade. Yet perceptual–motor coordination remains intact even for actions toward stimuli whose displacements are not perceived [10,11]. So, although spatial information about the location of objects cannot mediate perception of changes, it remains available at a motor level.

We recently demonstrated that a simple manipulation of the stimulus allows the perceptual system to regain access to precise spatial information: SSID largely disappears if a target is absent for a short temporal period when the eye stops at the end of a saccade [1,12,13]. Blanking a target during a saccade, and restoring it 50–300 ms later, restores the detectability of even quite small target displacements. This blanking effect occurs even for targets in darkness, implying that displacement detection under this condition relies on extraretinal signals rather than retinal information from the structured environment. The beneficial effect of blanking disappears if the target reappears before the saccade ends [1](Experiment 3) or if onset of the blank interval is delayed beyond the time range of SSID. In contrast to the interpretation of SSID that transsacadic information about spatial positions is poor, this effect

requires both the maintenance of high-quality information about pre-saccadic target position across the saccade, and a precise extraretinal signal.

These findings imply that information about pre-saccadic target position and precise extraretinal signals is available for stimulus localizations after the saccade, but they ordinarily are not used in perception. We have suggested that this is because the visual system assumes by default the stability of an object that is continuously available both before and after the saccade. A very large discrepancy between eye movement magnitude and image position is normally required to break this assumption. This assumption is also broken, however, when the object is not present immediately after the saccade, only under this condition are precise trans-saccadic information and extraretinal signals used to achieve displacement detection. Because of its strong effect in unveiling information available trans-saccadically, blanking presents a tool for studying visual stability and the nature of spatial information transferred across the saccade.

The blanking effect shows the importance of a stimulus that is present immediately after a saccade. According to our theoretical interpretation, the visual system seeks the saccade goal immediately after a saccade [14,15]. If this target is found within a certain spatial and temporal window, the visual system assumes it to have remained stable during the saccade, and the target becomes a 'reference object' to determine the positions of other objects and textures [1,16]. This reference object idea will be further investigated here, and the theory will be developed more fully in Section 6.

The aim of this study is to use the blanking effect to analyze the role of the immediate post-saccadic information in the maintenance of visual stability. We first investigate the effect of blanking on perceived stability in a more complex visual context consisting of two stimuli, a saccade goal and a distractor. For this situation, the reference object theory makes two predictions. First, in a two-object stimulus field, the visual system should exhibit a bias to perceive the saccade target as stable, and to attribute relative displacements to the distractor. Second, if one of the two objects is blanked beyond the critical temporal period, but the other is not, the continuously available stimulus should take the role of the reference object which is then seen as stable even if it jumps during the saccade-the jump should be attributed to the blanked object.

Experiment 1 examines the predicted interactions between the saccadic target and a distractor of similar size; blanking interval and jump are varied factorially. Experiment 2 establishes the minimum displacement size required to perceive the continuous stimulus as displaced when the other is blanked, while Experiment 3 examines the interaction between a small saccade target and a large background texture.

2. General methods

2.1. Subjects

Five paid subjects participated in Experiment 1 and 3, and six subjects in Experiment 2. Their ages ranged from 21 to 49 years. With one exception they were naive with respect to the object of the study, but all were experienced with the equipment from other eye-movement related tasks. Each performed at least three separate sessions in each paradigm. For each experiment, the results are based on 100–200 trials per condition from each subject. We used within-subjects designs in which all of the conditions of an experiment are replicated in each subject.

2.2. Apparatus

The experiments took place in a laboratory room providing an ambient illumination of approximately 0.1 cd/m^2. All stimuli were presented on a 21" video monitor (CONRAC 7550 C21) in combination with a TIGA graphics board (KONTRAST 8000). The monitor's spatial resolution was 1024×768 pixels at a frame rate of 100 Hz. Screen background luminance was set to 3 cd/m^2; the luminance of the stimuli was 25 cd/m^2. In order to assure that results were not affected by phosphor persistence, we measured the temporal decay of the phosphor luminescence with a linear PIN diode [17]. Due to the steady background luminance, contrast of the stimuli decayed to undetectable levels within 10 ms, excluding an effect of phosphor persistence on the data. In a previous experiment [1] (Experiment 2) we demonstrated that similar psychophysical effects are obtained in complete darkness, with fixation points and targets defined by a laser that could be turned on and off within a few microsec. Comparison of this experiment with our other experiments showed that phosphor persistence or visual frame effects did not have a measurable influence on the blanking effect.

The subject viewed the screen binocularly from a distance of 80 cm. Head movements were restricted by a biteboard and a forehead rest. Eye movements were measured with a SRI Generation 5.5 Purkinje-image eyetracker [18] sampled at 400 Hz. Its frequency response is better than 250 Hz with a noise level equivalent to about 20 arc/s/rms. The eyetracker can follow saccades of 15° or more without losing the eye.

Experiments were controlled by a 486 PC, which also performed automatic off-line analysis of the eye movement data in which saccadic latencies and saccade start and end positions were determined. The computer detected saccade onset by digital differentiation of the sampled eye position signal. Saccade-related sensory events were triggered when instantaneous eye velocity exceeded 30°/s. Early triggering is critical because of an unavoidable delay in Purkinje-image eyetracker records due to lens slippage within the eye [19] and a display delay of up to 10 ms because of screen raster sampling. Early triggering insured that stimulus modifications occurred before the eye reached maximum velocity.

2.3. Calibration and data analysis

Each session started with a calibration procedure: the subject sequentially fixated nine positions arranged on a circular array of 8° radius. The eyetracker behaved linearly within this range. Static accuracy of the eyetracker was better than 0.1°. Dynamically, however, the eyetracker registers a delayed saccade onset and artifactual overshoots at the end of each saccade due to the movement of the eye lens relative to the optical axis of the eye [19]. To determine direction of gaze, an off-line program searched the eye position record for the end of the overshoot and then calculated mean eye position over a 40 ms time window. The eye movement analysis program calculated latencies and start and landing positions of all saccades occurring in each trial.

2.4. Behavioral paradigm

In each trial a target jumped left or right 6 or 8°. The subject's task was to maintain fixation on the target, and to track it with a saccade as it jumped across the visual field. The two amplitudes and two directions were randomized and equally probable to minimize anticipation and adaptation by the subjects. Saccades beginning earlier than 100 ms or later than 400 ms after the target step were discarded. When the computer detected the saccade elicited by the first target step, a second, smaller jump and/or a blanking of either target or distractor was triggered (Fig. 1). All stimulus jumps occurred between single frames of the display. At the end of each trial, in a two-alternative forced choice procedure, the subject's task in Experiment 1 and 2 was to report which of two patterns, the target or a distractor, had moved during the saccade. In Experiment 3, the subject had to decide whether the target moved in the same direction as the saccade or in the opposite direction. The final position of the target served as the starting position for the next trial.

3. Experiment 1: interaction of target and distractor

In the first experiment we extend our previous analysis of the blanking effect to a situation where the saccade target and a distractor are present. One or the other stimulus could be blanked during and for a short period after the primary saccade. A blank period should prevent this object from being found and used as a reference object following the saccade. This object
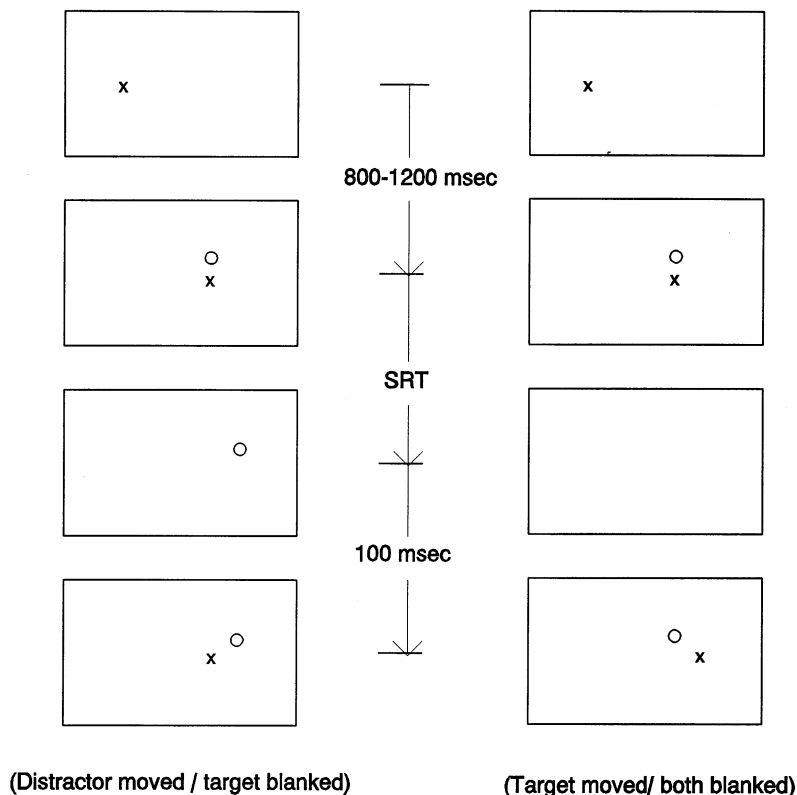
Fig. 1. Progress of a trial with blanking of target (left column) or both target and distractor (right column). Blanking duration is 100 ms. SRT: saccadic reaction time from target displacement to the start of the saccade.

should not be perceived as stable. We investigate the strength of this blanking effect, and also whether the object that was not the saccade target can function as a reference object. In this two-object environment, the visual system cannot take advantage of the normally correct generalization that the largest part of the visual field is the spatially stable part [5].

3.1. Method

Subjects began each trial by fixating a small x-shaped target, 0.2° in width (Fig. 1). After a random delay of 800–1200 ms the fixation was extinguished and the saccade target was presented, 6 or 8° in the visual periphery. Above this target appeared an outline circle of the same angular size, referred to as the distractor. The distractor's position was to be ignored for purposes of saccade targeting.

Before the saccade the target and the distractor were vertically aligned, but during the saccade one of them was displaced left or right so that vertical alignment was broken. Displacement magnitude was fixed at 0.5°. During and after the saccade either or both of the patterns could be blanked for a short temporal interval. Two displacement directions, times displacement of either pattern, times target blank/continuous presentation times distractor blank/continuous presen-

tation yielded 16 experimental conditions in factorial combination. The subject's task was to determine which of the two objects had jumped during the saccade, in a two-alternative forced-choice procedure. Subjects were explicitly instructed to report displacements, and to ignore blanking.

The blanking interval was set to 100 ms. In addition, eight of the conditions were repeated with a 50 ms blanking interval (Fig. 2). All 24 of the resulting conditions were run simultaneously in random order for each subject. All five subjects were experienced psychophysical observers; one of them (BB) was familiar with the aims of the experiment.

The matrix of results was analyzed with Statistica's MANCOVA routine. A single summary statistic was calculated for each subject in each condition and results analyzed between subjects. Separate analyses were done for target displacement and for distractor displacement conditions, since the number of cells was different in the two conditions. Data for all cells where one or both of the stimuli were blanked were entered as differences from the proportion correct in the corresponding no-blanking cell. Because the data are proportions, a square root arcsin transformation was applied to each cell. Specific contrasts were interpreted with *t*-tests.
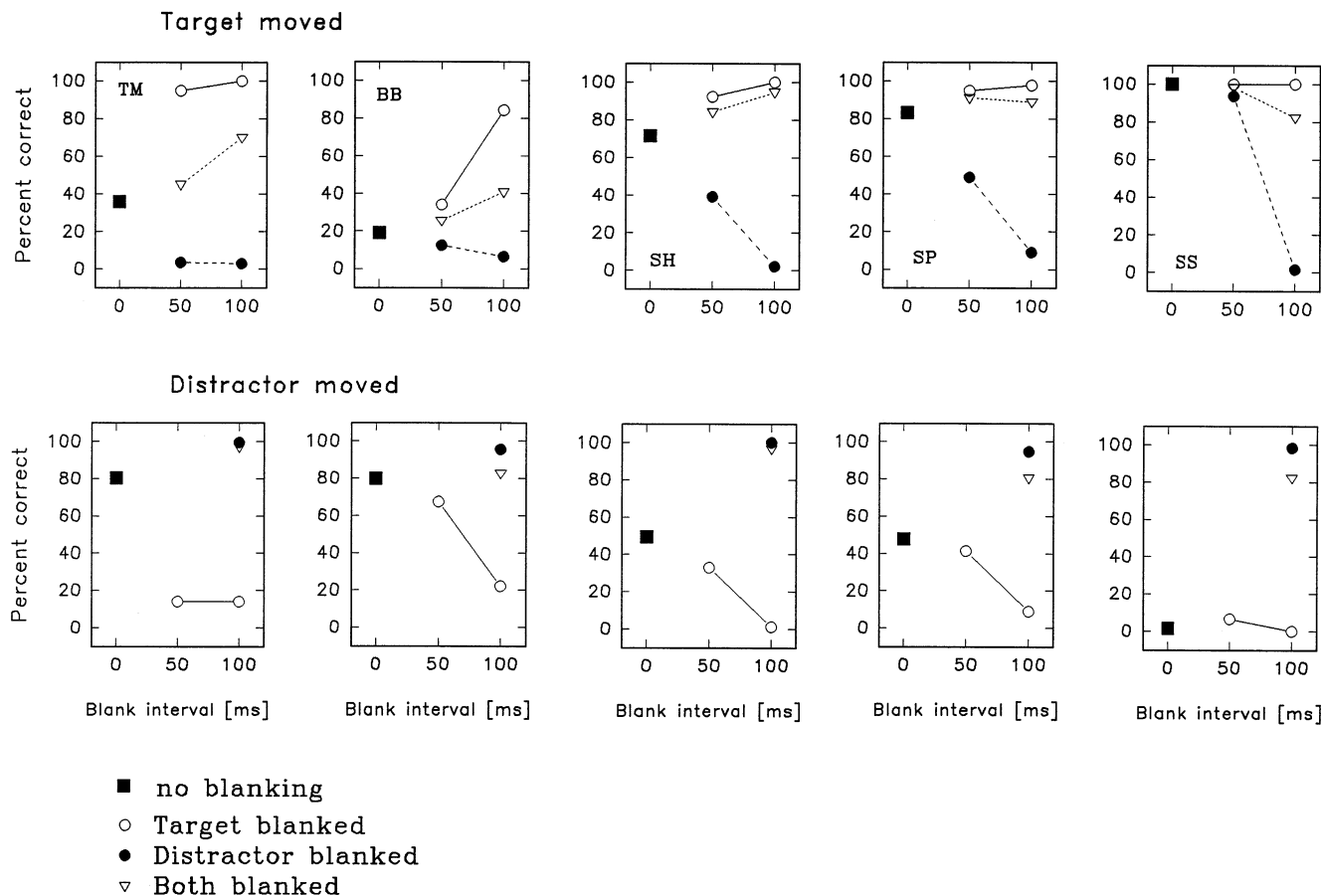
Fig. 2. Experiment 1. Each column depicts the performance of one subject when the target, the distractor, both, or neither are blanked, and when either the target or the distractor had been displaced (upper and lower graphs, respectively). The solid square at the left of each graph shows accuracy of the subject in correctly identifying a jump of the target (top graphs) or of the distractor (bottom graphs) when both were present continuously. Other points on each graph show accuracy when the target is blanked (open circles), when the distractor is blanked (filled circles), and when both are blanked (open triangles) for the intervals indicated on the horizontal axis. Each pair of graphs shows responses of one subject, ordered from left to right in decreasing order of percent correct when the distractor is moved.

3.2. Results

Four of the five subjects showed no consistent bias toward correctly detecting displacements in the direction of the saccade versus displacements in the opposite direction. The fifth subject (BB) was consistently more often correct for jumps in the direction opposite the saccade, but because this did not affect the overall pattern of results, the two directions of motion were collapsed in all subjects for further analysis and graphical display. Mean latency of the primary saccades to the appearance of the stimuli was 171.8 ± 44 ms (S.D.). Mean saccade amplitudes to the targets at 6 and 8° were 5.78 ± 0.61 and $7.56 \pm 1.0°$, respectively.

In the top row of Fig. 2 the target is displaced in each trial. The leftmost points in each graph (filled squares) represent subject bias when both stimuli were presented continuously, without blanking. There is a range of biases centered around an overall mean close to 50%, representing the tendencies of individual subjects to perceive motion of either the target or the distractor.

The two subjects below 50% show a bias of perceiving the distractor as displaced, while the other three subjects rather tend to attribute the relative displacement to the target. Thus, when both patterns are present continuously, there are large intersubject differences in preference for seeing either target or distractor as jumping, but a between-subjects t-test for matched pairs shows that the tendency to see the target move under the target-moved condition is not significantly different from the tendency to see the distractor move under the distractor-moved condition ($t_4 = 0.36$, $P = 0.73$).

The open circles in the top row of graphs in Fig. 2 result from including a blanking period for the target, while the distractor remains continuously present. The filled circles show the result of the converse manipulation, applying the blanking period for the distractor. All subjects tended to see the blanked stimulus as displaced, regardless of which was actually displaced. ANOVA showed that blanking had a significant effect for the conditions where the target was displaced ($F(2, 6) = 32.13$, $P < 0.001$). Because measures were

made at two blanking intervals, 50 and 100 ms, the effect of interval could also be tested. The effect of interval was not significant ($F(1, 3) = 0.045$, $P = 0.845$), showing that the blanking effect was not significantly stronger at 100 ms than at 50 ms. Thus the effects of blanking the target are already strong 50 ms after saccade detection. At the longest blank interval (right side of each graph in Fig. 2) the individual differences were considerably reduced, probably due to ceiling and floor effects. At this interval the difference between the target blanked and the distractor blanked conditions was statistically significant (t-test for matched pairs, $t_4 = 19.98$, $P < 0.001$).

An analogous result was found when the distractor was displaced, as shown in the bottom row of graphs in Fig. 2. Again the main effect of blanking was statistically significant ($F(2, 6) = 137.4$, $P < 0.0001$). The target was seen as jumping if it was blanked, resulting in a low percent correct; if the distractor was blanked, however, it was almost always perceived correctly if it indeed jumped. Again the difference is statistically significant for a 100 ms blank ($t_3 = 16.72$, $P = 0.0005$).

When both target and distractor were given identical blanking periods, the blanking induced a slight but significant tendency to identify the jumped stimulus more accurately, whether it was the target (inverted triangles in Fig. 2, top) or the distractor (bottom). For statistical analysis the difference between the percent correct in the 100 ms blanking condition and in the corresponding no-blank condition was calculated for both the target-moved and the distractor-moved paradigms, and the resulting data averaged in each subject. A between-subjects t-test for matched pairs showed a significant enhancement in accuracy ($t_4 = 5.75$, $P = 0.0045$) demonstrating that blanking increases the subjects' accuracy even when both patterns are given the same blanking intervals. The intermediate blanking interval was not run for the conditions shown at the bottom in Fig. 2.

3.3. Discussion

The results from the 24 conditions probed here can be described compactly in a few generalizations. First, without any blanking the saccade target has no systematic advantage to obtain the role as a stable reference over the distractor; some subjects then rather perceive the target as displaced, while others tend to see the distractor moving. Second, whatever stimulus has a blank is more likely to be seen as displaced, whether that stimulus was actually displaced or not-space constancy is extended preferentially to objects that remain in the visual field throughout a trial, regardless of which pattern actually jumped. Third, even a brief blank interval has a strong effect. The effect of blanking the target appears gradually, not abruptly, though it

is clearly present even at 50 ms. Finally, a blank interval improves performance when the entire configuration is blanked, again with a tendency for a longer blank to yield a greater advantage.

The data from Experiment 1 clarify the role of post-saccadic target information and context in space constancy. First, they confirm our previous results that the presence or absence of a stimulus immediately after a saccade determines whether extraretinal eye position information and information stored in trans-saccadic memory are discarded or used for spatial localization [1]. This is reflected in the finding that a blank interval improves performance when it is extended to both of the two stimuli. Our interpretation is that blanking both stimuli simply allows the visual system to process both stimuli in the same way, allowing the blanking effect to overcome the tendency to perceive an object as stable regardless of its actual intra-saccadic displacement. Only when no visual information is available after saccade end is extraretinal information used in the perception of displacement. In our experiment the motion transient of the continuous but displaced object was masked by saccadic suppression, so that the transient did not affect judgments of which object had been displaced.

Second, and more importantly, the data demonstrate that immediate post-saccadic information determines whether objects are perceived as stable or as moving across the saccade-presence within the first 50 ms after a saccade is crucial for a stimulus to become the spatial reference. Accordingly, the object that is present in the visual field in the critical time when the eye lands is always perceived as stable-displacements are consistently attributed to the blanked target. Thus, in this case, extraretinal information is of no importance; perception of stability is dominated by presence and spatial position of the continuous (reference) object. This is demonstrated by the strong illusions of trans-saccadic instability through manipulation of the immediate post-saccadic stimulus.

Finally, the results speak against our previous prediction that the saccade target rather than the distractor should be perceived as stable; at least for the two-stimulus configuration with closely spaced target and distractor used in this experiment both stimuli are equally likely to be seen as stable.

4. Experiment 2: spatial limits for displacement discrimination

The first experiment demonstrated that a manipulation of immediate post-saccadic visual information can lead to the illusory perception of displacements of other, temporarily blanked objects. The induced effects are amazingly large and consistent; with a 0.5° displace-
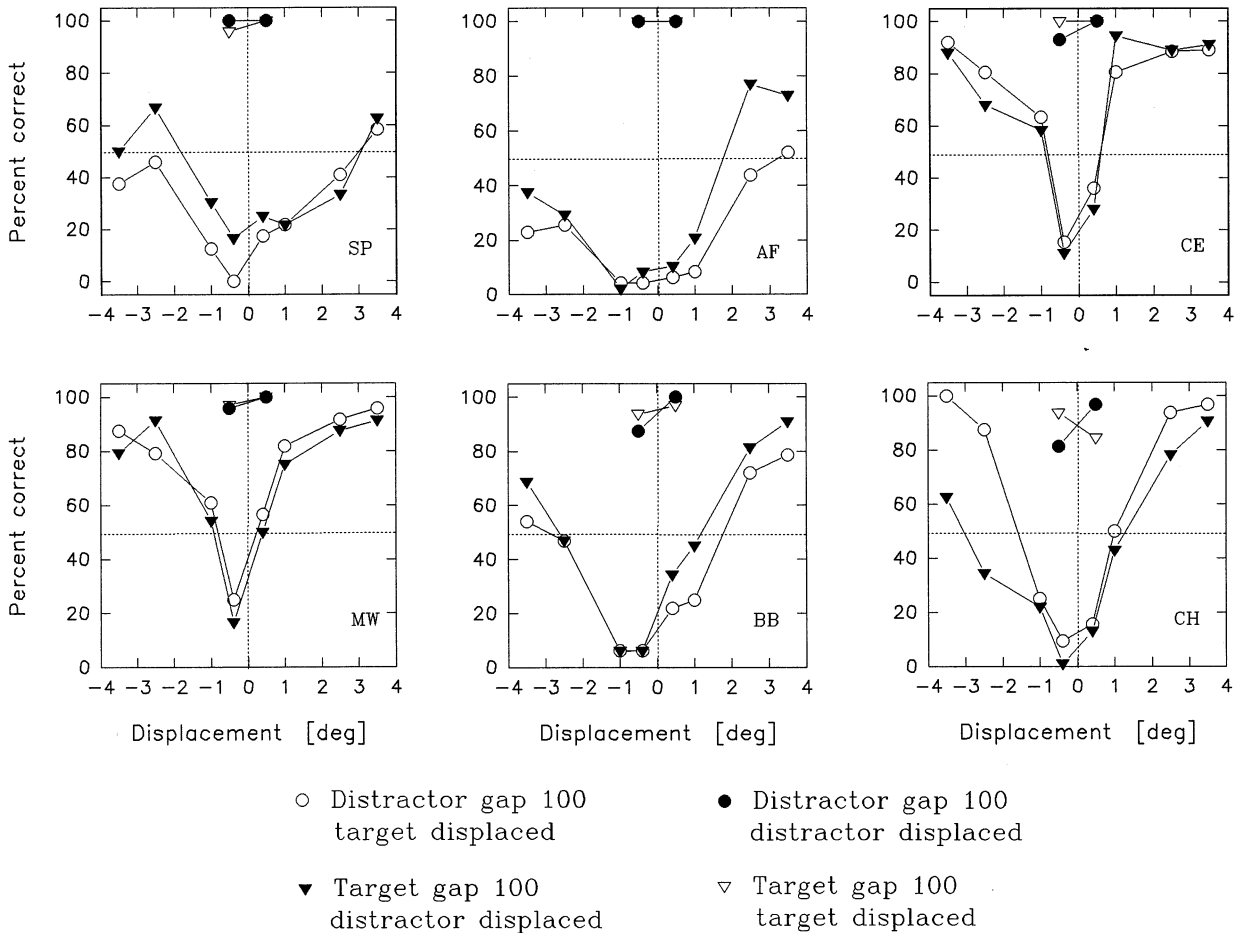
Fig. 3. Experiment 2. Percent correct discrimination of one of two patterns as displaced when the other pattern is blanked. Negative displacements indicate that stimulus displacement and saccade occurred in opposite directions.

ment and a 100 ms blank, biases for perceiving the blanked object as moving approached 100% in all subjects. Experiment 2 expands the range of displacements under these conditions to find a displacement large enough to overcome the tendency to perceive a continuous (but shifted) target as stable. With this experiment we titrate the stabilizing effect of the temporal continuity of the reference object against the calibrating effect of extraretinal information that indicates stationarity of the blanked (undisplaced) object. The effects of extraretinal signals are in equilibrium with the assumption of stability of continuous targets when the displaced (but continuous) stimulus is seen as moving 50% of the time.

4.1. Method

During the primary saccade one of the two visual objects jumped while the other was blanked. Gap duration was fixed at 100 ms. For the conditions where the continuously presented object was displaced, displacement magnitude was varied in a range from -3.5 to $+3.5°$ in steps of 0.5–1°. From the results of the

previous experiment we expected close to perfect performance for the cases where the blanked object is also displaced; therefore, in these conditions only displacement magnitudes of $\pm 0.5°$ were applied. Two subjects from Experiment 1 and four new subjects were run. Other methods are as described above.

4.2. Results

Mean latency ($\pm$ S.D.) of the primary saccades to the appearance of the stimuli was 176.5 ± 32.2 ms. Mean saccade amplitude to the targets at 6 and 8° was 5.8 ± 0.44 and $7.78 \pm 0.58°$, respectively.

Fig. 3 shows the performance of the six subjects in correctly attributing the displacement to the jumped stimulus. It can be seen that for the cases where the continuous stimulus was displaced (open circles and solid triangles) the jump had to be very large, over 50% of the saccade size, to be reliably perceived. An ANOVA computed for these cases showed a significant main effect of displacement size ($F(7, 35) = 26.8$, $P < 0.001$). Functions for target and distractor were not significantly different ($F(1, 5) = 0.05$). Two of the sub-

jects (AF and SP, Fig. 3) did not perceive the continuously present patterns to jump even at the largest (inward) displacement of −3.5°. For all subjects the minimum of the function was reached when the pattern actually jumped slightly in the direction opposite the saccade, by 0.5–1°.

In contrast, all subjects correctly perceived displacement of a stimulus, either distractor or target, if that stimulus was blanked. Discrimination was nearly perfect even at the small displacement magnitudes of ± 0.5° (short lines near the top center of each graph in Fig. 3). This replicates the result of Deubel et al. [1] in the presence of a second pattern.

Due to the relatively large stimulus displacements applied in the trials where the continuous stimulus was displaced, the subjects produced secondary, corrective saccades in 74% of these cases. The question arises whether these corrective saccades are directed—as instructed—to the target. Fig. 4 shows the mean amplitudes of corrective saccades as a function of stimulus displacement, for the cases where the continuously present stimulus–either target or distractor–was displaced. Negative amplitude values indicate displacements opposite to the primary saccade detection. It can be seen that size and direction of the corrective saccades correlates well with displacement size when the target was displaced (open symbols). When the distractor was displaced, however, corrective saccade size was unaffected (solid symbols). The data clearly show that the secondary saccades are always correctly directed to the instructed target. Nevertheless, in these cases, the subjects systematically misattribute the displacement to the blanked stimulus (Fig. 3). This indicates that the oculomotor system and the perceptual system access different types of information.
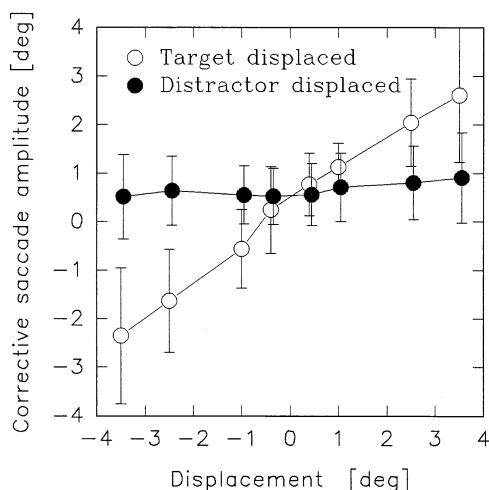

Fig. 4. Experiment 2. Amplitudes of corrective saccades as a function of size and direction of stimulus displacement. Negative displacements indicate stimulus jumps opposite to the primary saccade (backward displacements).

4.3. Discussion

The large displacement magnitude at which intra-saccadic jumps can overcome the blanking effect indicates the very poor sensitivity of subjects to displacements of continuously present stimuli in the presence of a blanked object. That is, only at this amplitude subjects correctly perceive the object as jumping despite the stabilizing effect of its continuous presence. The system seems biased to accept the position of a saccade target to be constant if it is continuously present, even for stimulus displacements on the order of half the size of the saccade.

The finding that the secondary saccades are corrective in the sense that they are all directed to the target demonstrates that visual stability and the perception of intra-saccadic displacements are independent of oculomotor behavior; obviously, the subjects cannot make use of information about correction saccade amplitude for determining whether target or distractor were displaced.

5. Experiment 3: shift of visual background texture

Visual target positions are normally evaluated relative to a visual context of background objects, textures and surfaces. Under normal perceptual conditions, the background might take the role of the reference. In this experiment we examine the influence of a larger and more complex visual field on the localization of a small blanked target. The question arises whether the visual system can use this larger visual background to recalibrate post-saccadic target position. Intra-saccadic displacements of the background should then be misattributed to target displacements.

5.1. Method

In addition to a target, we presented a background pattern of 14–16 elliptical shapes (Fig. 5a). The ellipses appeared in a circular area around the target that extended about 6° in diameter. This background pattern remained the same throughout a trial, but could be displaced as a whole during the primary saccade (Fig. 5b). The background pattern was presented continuously, and in randomly ordered trials it was displaced upon saccade detection either 0.75° to the right, 0.75° to the left, or not at all. The target was always blanked for 200 ms, beginning at the same time as the background shift, and was shifted in a range from −1.0 to +1.0° in 0.5° increments. Subjects indicated whether the target had moved either in the same direction as the saccade (forward) or in the opposite direction (backward).
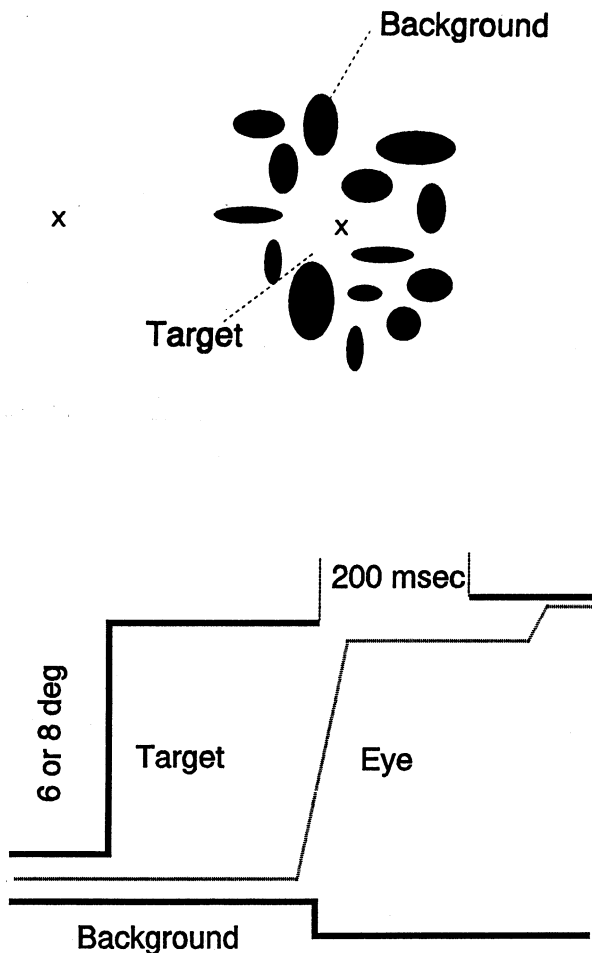
Fig. 5. Experiment 3. Top: stimulus configuration. Only the target was blanked, and the background was present continuously. Bottom: position (vertical axis) versus time (horizontal axis) during a trial. The background jump and the start of target blanking coincide with the detection of the saccade.

5.2. Results

Mean latency (± S.D.) of the primary saccades to the appearance of the stimuli was 175 ± 34.7 ms. Mean saccade amplitude to the targets at 6 and 8° was 5.77 ± 0.66 and 7.63 ± 0.91°, respectively.

Fig. 6 shows the discrimination results for five subjects. The graphs display percent 'forward' judgments (in the same direction as the primary saccade) as a function of displacement size and background displacement. Though subjects reported to have never perceived the intra-saccadic displacement of the background, the displacement had a consistent effect on perceived target jumps, shifting the psychometric functions in the direction of the background displacements.

The magnitude of the interaction of target with background can be estimated by examining the deviation of the curves for leftward and for rightward displacement of the background where they cross the 50% 'neutral' position (horizontal dashed line in each graph in Fig.

5). For a further statistical analysis we fitted each psychometric function separately with a cumulative gaussian and calculated the 50% point, i.e. the actual target displacement where the subjects perceived a perfectly stable target. In other word, these are the target displacements that are necessary to compensate for the effect of the background shift on displacement detection. The results are displayed in Fig. 7, showing this target displacement as a function of the background jump. The average total effect in the judgments is 0.73°, a figure that estimates the effect of a 1.5° difference in background positions. Thus 48.7% of the background shift is reflected in target position judgments. It is important that the background displacement did not eliminate the perceptual advantage of blanking; it merely biased the judgments of displacement, which still took place with low thresholds and with the steep psychophysical functions that have characterized the blanking effect in our other experiments.

The effect is analogous to induced motion, with apparent target displacement being biased in the direction opposite the background displacement. The result implies that target location is evaluated with reference to the continuously visible background when the target is blanked after the saccade.

5.3. Discussion

Displacement of the background had a strong effect on target localization, even though the background displacement itself was not perceived due to saccadic suppression. Displacement discrimination was biased, in the sense that perceived forward target displacements were sometimes seen in the presence of backward background displacements. The subjects described this as an apparent motion of the target, which is surprising given the fact that the pre-saccadic pattern was in the retinal periphery and the post-saccadic pattern was centered near the fovea. The effect can be interpreted as a form of trans-saccadic induced motion; the subjects perceive an apparent target motion with respect to a stable background despite the fact that both the target and background undergo a displacement of about 6° on the retina due to the saccade. The relative positions of target and background in space, rather than on the retina, determine what is perceived across the saccade.

The magnitude of the interaction of target with background can be estimated by examining the deviation of the curves for leftward and for rightward displacement of the background showing that 48.7% of the background shift is reflected in target position judgments. This is close to the estimate of Bridgeman and Graziano [20] that half of an intra-saccadic background deviation transfers to perceived visual target position, if the background has texture but no meaningful structure. The consistency of these two estimates, despite
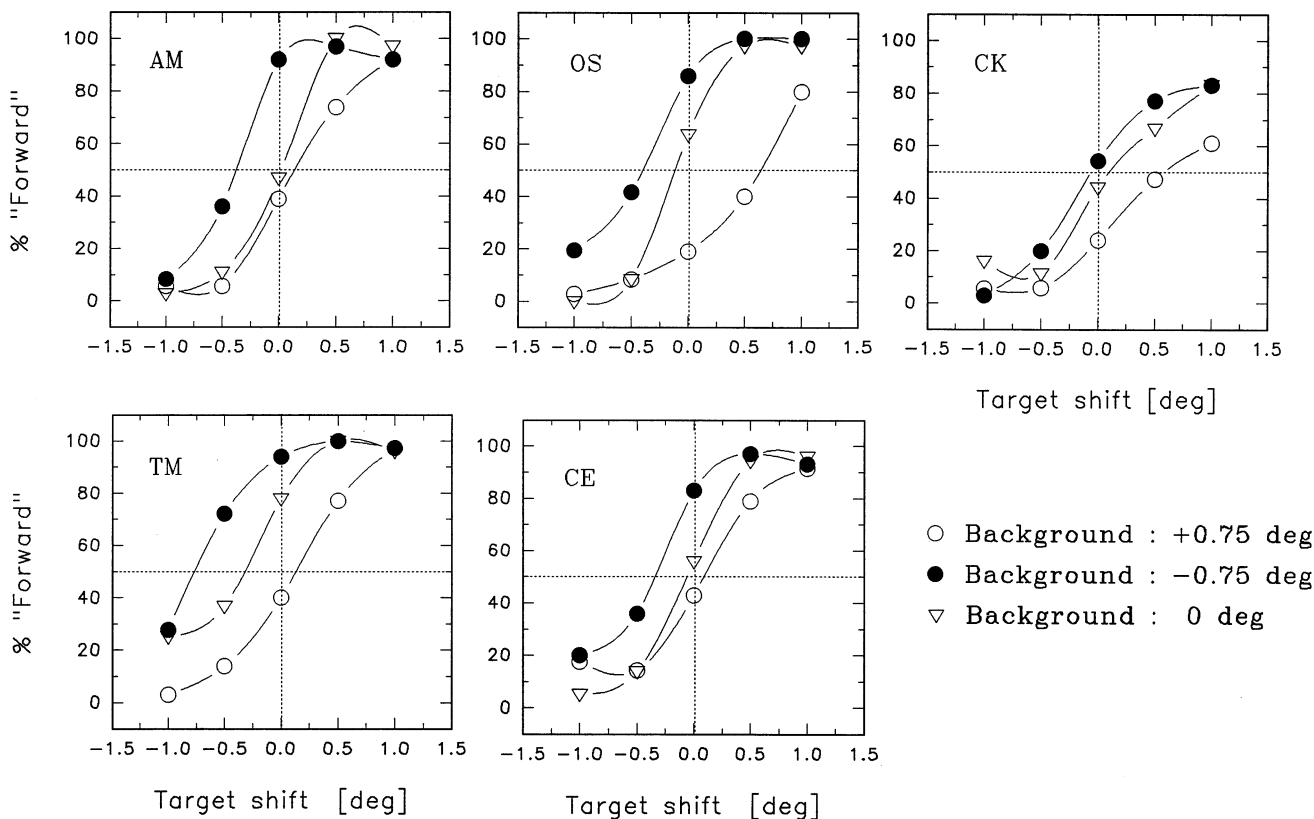
Fig. 6. Experiment 3. Proportion of judgments that the target jumped in the same direction as the main saccade, when the background was held steady, displaced in the direction of the saccade, or displaced in the opposite direction. Each graph shows data from one subject.

differences in method and background texture, suggests that background texture parameters are relatively unimportant, as long as the background has a large area.

Honda [21] also found that background is important in stabilizing perception trans-saccadically: the presence of a background results in smaller and briefer mislocalization errors. And as noted above, perceptual space constancy is generally more robust in a complex visual field [22]. These results in combination with ours speak

Fig. 7. Experiment 3. Perceived shift of the blanked target induced by the background shift.

for an explanation of the mechanism of the blanking effect at a central level that integrates retinal location, extraretinal signals and visual context information.

6. General discussion

This study addresses two theoretical issues: the trans-saccadic integration of visual information, and the general problem of oculomotor space constancy (the appearance of a stable visual world despite movements of the eyes). These problems are often treated separately, but our findings suggest that both are necessary components of the more general problem of perceptual continuity. In the present context this issue reduces to the questions of how spatial orientation can be maintained across saccadic eye movements, and how a stable and consistent visual world can be perceived across the discontinuities of the retinal image due to saccades. Theories of what information is transferred across saccades can be placed on two dimensions, beginning with a theory that only semantic or symbolic information is transferred [23,24,37]. On one dimension, the semantic theory can be contrasted with object-oriented theories and data. These theories support the availability of quantitative spatial information transfer across the sac-
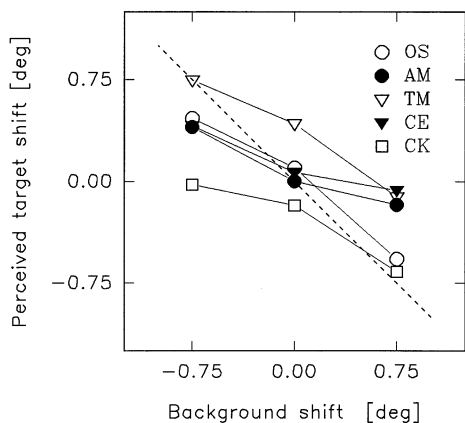
cade, but only about a small number of visual objects [25,26]. These objects must be subjects of visual attention to be transferred to the next fixation.

The second dimension contrasts the semantic theory with theories that handle visual space as a continuum. Saccadic displacements are corrected with a series of vectors, allowing quantitative compensations for the coordinate shifts produced during saccades [2,27]. For this dimension the correction is not of objects but of space itself, or of the entire image as a unit, regardless of its content. These theories are the traditional accounts of space constancy across saccades.

The evidence presented here forces a move away from the interpretation of perceptual space constancy as a quantitative compensation and toward a more object-oriented conception. The existence of SSID, measured quantitatively since the 1970s, already implied that a quantitative compensation by extraretinal signals could not be responsible for space constancy, for stimulus displacements of several degrees could go unnoticed during large saccades, but our perceptual calibration is far better than this. However, the theoretical implications of this discrepancy did not result in a new theory of space constancy at the time.

The present data can best be interpreted in terms of a reference object theory that has emerged recently. Several versions of this theory have been described [1,15,16]. In our previous paper [1], we were led to such a theory by our data on the blanking effect. In that paper we found that blanking a target during and just after a saccade greatly reduced the threshold for detecting its intra-saccadic displacement, even though such a blanking actually interferes with displacement detection during fixation. We explained these phenomena by suggesting a three-stage process of recalibrating visual space after a saccade. First, a particular object is selected as a target for a future saccade. This object receives preferential perceptual processing equivalent to an obligatory shift of attention to the target stimulus [28]. Second, higher-level visual features (geometric properties, etc.) of this reference object are stored in memory so that it can be identified after the saccade. Third, the visual system seeks the target after fixation is re-established, comparing the stored features with the new image. If a match is found, the matching object is identified as the reference object, other parts of the new visual scene are localized relative to it, and no further computation or comparison takes place [9]. Extraretinal signals do not enter into this process. The data presented here suggest that this mechanism relies on the visual information available immediately after the saccade-the initial 50 ms are crucial for space constancy.

Several lines of research provide evidence consistent with this theory, and inconsistent with other theories of space constancy. The reference-object theory requires only relatively little information to be stored from previous fixations; confirming this prediction, only qualitative information about most of the visual field is available [26]. For example, a visual scene can be moved or changed in size [16], or objects in a scene can be moved or replaced by other objects [29], and the changes are not detected if they occur during saccades. The extensive SSID literature confirms this property of inter-saccadic integration. Only changes in the saccade goal and possibly a few other attended objects are transferred accurately across saccades [26,37]. The mechanism concentrates on the region near the saccade target, with only secondary influence from other locations [15].

The present experiments provide a more detailed characterization of the timing of the trans-saccadic integration process. The results suggest that the presence or absence of an object at the moment when the eye lands is an essential determining factor for that object to become a spatial reference. This implies that the reference object need not be the saccade target: another nearby object can take that role, if the saccade target is blanked so that it is unavailable for establishing a new calibration. The distractor's displacement is not visible if it is continuously present; rather, the motion is attributed to the blanked saccade target. This demonstrates that temporal continuity of an object is more important even than selection as a saccade target in establishing a reference object. In like manner, our third experiment shows that a stimulus array that is not blanked will be perceived as stable even if it is displaced, as long as the saccadic target is blanked. The 'background' array takes on the role of the reference object, again because of its temporal continuity.

These results necessitate a modification of the reference object theory that we described earlier [1,16]. The visual system need not be committed to a single identified reference object before the saccade begins, for a non-target object can become the reference object, and the system does not know in advance which object will be appropriate as the reference object. According to our data, at least two objects near the saccade goal region might also serve as reference objects, and the assignment of stationarity depends upon which one is found after the saccade. This is consistent with indications that information about three to four objects can be localized across a saccade [26]. Whether an object is defined in advance as target or distractor seems to play little role in the post-saccadic determination of the reference object.

Nevertheless, there is some independent evidence that the saccade goal target has a special role in post-saccadic visual calibration. Bischof and Kramer [30], for instance, found perceived locations to be corrected more quickly near the saccadic goal than at other retinal positions. In a saccadic suppression experiment, Heywood and Churcher [31] showed that subjects often

misattribute an intra-saccadic displacement of the saccade goal to a displacement of another visual object such as the previous fixation, tending to preserve space constancy preferentially for the saccade goal. Finally, Ross et al. [32] demonstrated that stimuli flashed shortly before a saccade are mislocalized such that they are perceived close to the saccade target. Whether this 'spatial attraction' by the saccade target is reminiscent of the effect of our 'reference object' mechanism that tries to anchor pre-saccadically attended objects on the target found after the saccade must be clarified by further research.

Another refinement of the theory is made possible by our result with two blanked objects. If both stimuli are blanked, performance is better than if neither is blanked. This is quite unexpected at first glance, since spatial information must be held in trans-saccadic memory for a longer period, and delay should lead to decay of performance. However, it is consistent with findings from our previous work on the blanking effect. In that work, detectability of intra-saccadic target displacements was even better than the detectability of similar displacements during fixation. With target blanking, displacement detection seems to be aided by information that is not available if the reference object is found. In the experiments where two objects are blanked, no object receives an advantage over the other, but localization of both targets is aided by the availability of extraretinal information that is discarded if a reference object is found. There is no reason for the visual system to still assume visual stability for either object, because neither is found immediately after the saccade.

Taken together, our results can be combined with earlier evidence to suggest that space constancy depends on comparison of common elements in the pre- and post-saccadic images. This comparison takes place in a 'constancy window' that is about 50 ms in duration and has a size that can reach more than 50% of the size of the saccade, depending on stimulus conditions. Neither the spatial nor the temporal limits can be exceeded if constancy is to be maintained.

Neurons in lateral intraparietal cortex (LIP) described by Duhamel et al. [33] may be performing some of the computations required by our theory. Receptive fields in this area shifted to compensate for a saccade about 80 ms before the start of the movement. Thus the LIP seems to store pre-saccadic, visual information across the saccades and possesses quantitative spatial information about the saccade. Similar properties have been recently reported from neurons in the superior colliculus [34].

Our finding that corrective saccades are generally accurate, even when the perceptions of displacements of the targets to which they are directed are grossly in error, highlights a difference between cognitive and sensorimotor visual functions. Several authors have differentiated a cognitive or perceptual system, governing visual experience and pattern recognition, and a sensorimotor system, controlling visually guided behavior [10,35,36]. Bridgeman et al., Paillard, and Milner and Goodale show that motor information can be accurate even under conditions where perception is in error. Our present result shows a conclusion also reached by these authors: information can flow from the cognitive to the sensorimotor systems, under some conditions, making the sensorimotor function inaccurate; but information cannot flow the other way, using accurate motor planning information to inform the cognitive system about locations of objects in space.

References

[1] Deubel H, Schneider WX, Bridgeman B. Post-saccadic target blanking prevents saccadic suppression of image displacement. Vis Res 1996;36:985–96.

[2] Holst von E, Mittelstaedt H. Das Reafferenzprinzip: Wechselwirkungen zwischen Zentralnervensystem und Periphere. Naturwissenschaften 1950;37:464–76.

[3] Grüsser HJ, Krizic A, Weiss LR. Afterimage movement during saccades in the dark. Vis Res 1987;27:215–26.

[4] Bridgeman B. Extraretinal signals in visual orientation. In: Prinz W, Bridgeman B, editors. Handbook of Perception and Action, vol. I:Perception. London: Academic Press, 1995:191–223.

[5] Gibson JJ. The Senses Considered as Perceptual Systems. Boston: Houghton Mifflin, 1966.

[6] Helmholtz von H. Handbuch der Physiologischen Optik, 3. Leipzig: Voss, 1866.

[7] Mack A. An investigation of the relationship between eye and retinal image movement in the perception of movement. Percept Psychophys 1970;8:291–8.

[8] Bridgeman B, Hendry D, Stark L. Failure to detect displacement of the visual world during saccadic eye movements. Vis Res 1975;15:719–22.

[9] Bridgeman B, Van der Heijden AHC, Velichkovsky BM. A theory of visual stability across saccadic eye movements. Behav Brain Sci 1994;17:247–92.

[10] Bridgeman B, Lewis S, Heit G, Nagle M. Relationship between cognitive and motor-oriented systems of visual position perception. J Exp Psychol Hum Percept Perform 1979;6:692–700.

[11] Prablanc C, Martin O. Automatic control during hand reaching at undetected two-dimensional target displacements. J Neurophysiol 1992;67:455–69.

[12] Deubel H, Schneider WX. Can man bridge a gap? Behav Brain Sci 1994;17:259–60.

[13] Deubel H, Schneider WX, Bridgeman B. Stimulus blanking diminishes saccadic suppression of image displacement. Invest Ophthalmol Vis Sci 1994;35:2033.

[14] Deubel H, Wolf W, Hauske G. The evaluation of the oculomotor error signal. In: Gale AG, Johnson FW, editors. Theoretical and Applied Aspects of Eye Movement Research. Amsterdam: Elsevier, 1984:55–62.

[15] Irwin DE, McConkie G, Carlson-Radvansky L, Currie C. A localist evaluation solution for visual stability across saccades. Behav Brain Sci 1994;17:265–6.

[16] McConkie G, Currie C. Visual stability across saccades while viewing complex pictures. J Exp Psychol Hum Percept Perform 1996;22:563–81.

[17] Wolf W, Deubel H. P31 phosphor persistence at photopic mean luminance level. Spat Vis 1997;10:323–33.

[18] Crane HD, Steele CM. Generation-V dual-Purkinje-image eye-tracker. Appl Opt 1985;24:527–37.

[19] Deubel H, Bridgeman B. Fourth Purkinje image signals reveal lens deviations and retinal image distortions during saccadic eye movements. Vis Res 1995;35:529–38.

[20] Bridgeman B, Graziano J. Effect of context and efference copy on visual straight ahead. Vis Res 1989;29:1729–36.

[21] Honda H. Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. Vis Res 1993;33:709–16.

[22] Matin L, Picoult E, Stevens JK, Edwards M W Jr, Young D, MacArthur R. Oculoparalytic illusion: Visual-field dependent spatial mislocalizations by humans partially paralyzed with curare. Science 1982;216:198–201.

[23] O'Regan JK, Levy-Schoen A. Integrating visual information from successive fixations: does trans-saccadic fusion exist? Vis Res 1983;23:765–8.

[24] O'Regan K. Solving the 'real' mysteries of visual perception: the world as an outside memory. Can J Psychol 1992;46:461–88.

[25] Hayhoe M, Lachter J, Feldman JA. Integration of form across saccadic eye movements. Perception 1991;20:393–402.

[26] Irwin DE. Memory for position and identity across eye movements. J Exp Psychol Learn Mem Cogn 1992;18:307–17.

[27] Sperry R. Neural basis of the spontaneous optokinetic response produced by visual inversion. J Comp Physiol Psychol 1950;43:482–9.

[28] Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. Vis Res 1996;36:1827–37.

[29] Pollatsek A, Rayner K, Henderson JM. Role of spatial location in integration of pictorial information across saccades. J Exp Psychol Hum Percept Perform 1990;16:199–210.

[30] Bischof N, Kramer B. Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. Psychol Forsch 1968;32:195–218.

[31] Heywood S, Churcher J. Saccades to step-ramp stimuli. Vis Res 1981;21:479–90.

[32] Ross J, Morrone MC, Burr DC. Compression of visual space before saccades. Nature 1997;386:598–601.

[33] Duhamel J, Colby C, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. Science 1992;27:227–40.

[34] Walker MF, Fitzgibbon EJ, Goldberg ME. Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. J Neurophysiol 1995;73:1988—2003.

[35] Paillard J. Cognitive versus sensorimotor encoding of spatial information. In: Ellen P, Thinus-Blanc C, editors. Cognitive Processes and Spatial Orientation in Animal and Man. Dordrecht, Netherlands: Martinus Nijhoff, 1987.

[36] Milner AD, Goodale MA. The Visual Brain in Action. Oxford: Oxford University Press, 1995.

[37] Irwin DE, Andrews RV. Integration and accumulation of information across saccadic eye movements. In: Inui T, McClelland JL, editors. Attention and Performance, vol. XVI. Cambridge: MIT Press, 1995:125–55.