Vision Research 50 (2010) 249–259

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Landmarks facilitate visual space constancy across saccades and during fixation

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ARTICLE INFO

Article history:
Received 28 July 2009
Received in revised form 10 September 2009

Keywords:
Saccades
Space constancy
Efference copy
Eye movements
Saccadic suppression

ABSTRACT

It has been demonstrated that visual objects that are present after saccadic eye movements act as landmarks for the localization of stimuli across saccades, facilitating space constancy (Deubel, 2004). We here study the temporal conditions under which landmark effects occur after saccadic eye movements, and during fixation. Two small objects were presented 6° in the periphery, one above the other. Observers saccaded to the space between them. One of the objects disappeared during the saccade and reappeared with a variable delay during or after the saccade. At the same time either that object or the continuously present one jumped by 1°. The observer's task was to decide which object had moved. The results revealed a strong bias to assign movement to the object that was blanked, regardless of which actually moved. If both objects were blanked, the one that was blanked for a shorter time tended to be seen as stable. The effects were stronger as the onset asynchrony between the stimuli increased. Surprisingly, analogous though weaker effects occurred during visual fixation, suggesting that similar visual mechanisms relying on visual landmarks operate both across saccades and during fixation.

1. Introduction

The visual world appears continuous, and we do not perceive saccade-induced interruptions of visual information. We also perceive the world as stable, despite the fact that the images of objects drastically change their retinal positions during each saccadic eye movements. How does the visual system achieve perceptual continuity and space constancy?

Early theories of space constancy were based on cancellation, where an oculomotor efference copy is subtracted from the retinal motion (Sperry, 1950; von Holst & Mittelstaedt, 1954). It had been assumed that the world appears stable because the visual system encodes the size and the direction of a saccade into a neural signal coding extraretinal eye position information. Following each saccade, the visual system subtracts the extraretinal signal from the retinal image shift to re-map perceived position.

Evidence for such a remapping mechanism came from single neurons in the monkey parietal cortex that anticipate the retinal consequences of a saccade (Duhamel, Colby, & Goldberg, 1992). Indeed, a cell began to fire before a saccade carried an object into the cell's receptive field. The firing was maintained up to 50 ms after the end of the eye movement, even when the object was extinguished. This spatial processing mechanism for visual information could be activated only by a saccade and not by the allocation of attention. The neural activity was interpreted as a transsaccadic memory of a retinotopically coded stimulus which is used with each fixation to generate a continuously accurate representation of the visual space.

Other work has shown that these cancellation mechanisms alone cannot be responsible for space constancy, because extra-retinal information about object location has proved to be rather inaccurate. Further, the gain of the extraretinal eye position signal is too low to support space constancy even during steady fixation (Bridgeman, 2007; Stark & Bridgeman, 1983) and its dynamics are too slow to keep up with saccades (Ilg, Bridgeman, & Hoffmann, 1989). If space constancy arose through a cancellation, each inaccuracy of the extra-retinal information would result in a disturbance of space constancy. However, in everyday life we perceive objects that are continuously available as stable. It has been proposed that the visual system has a built-in assumption or 'null hypothesis' to prevent disturbance of constancy, so that failings of the imperfect cancellation mechanism are inhibited by saccadic suppression and supplemented by a visual system which assumes that the world does not change during saccadic eye movements (MacKay, 1962; see also Bridgeman, van der Heijden, & Velichkovsky, 1994).

However, this assumption also results in a reduced ability to detect target displacements during saccades. During fixation, a target jump activates motion detectors that allow us to perceive movements of objects. During saccades, however, a saccadic suppression mechanism diminishes these motion signals and additionally the 'null hypothesis' applies. Consequently, the world generally

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doi:10.1016/j.visres.2009.09.020

appears stable. Several experiments have supported the inability to displacement during the eye movement up to an amount of one-third the saccadic amplitude (e.g., Bridgeman, Hendry, & Stark, 1975; Deubel, Schneider, & Bridgeman, 1996).

The existence of a 'null hypothesis' does not clarify whether exact information about initial target position is in general unavailable to the visual system or whether the information is not used for detecting target displacement when the saccadic eye movement is finished and the target is visible. However, Deubel et al. (1996) demonstrated that a short blanking of a target in the absence of other objects produces a strong improvement of displacement detection ('blanking effect'). The interruption in presentation therefore must evoke precise information about the pre-saccadic target position. Accurate extra-retinal signals that are stored over the eye movement but not normally accessible to perception are now available. This stored information is not used if the target is visible at the end of the saccade. The post-saccadic blanking effect has been replicated, even for objects that displace in directions not collinear or orthogonal to the saccade (Gysen, Verfaillie, & DeGraef, 2002b).

In this context, Deubel (2004) and Deubel, Schneider, and Bridgeman (1998) also found that another object present at the end of a saccade could serve as a reference or landmark object for the post-saccadic relocalization of a blanked target; the continuously present landmark shows a strong tendency to space constancy, being perceived as stationary. If the landmark is visible both before and at the end of the saccade, target localization depends predominantly on the pre-saccadic relative distances between the reference object and the target. As a result, a landmark object that is displaced during a saccade induces a displacement sensation for an unmoved target that reappears after some temporal blanking after the saccade. Further, objects close to the saccade target or vertically aligned with it are particularly effective as spatial references (Deubel, 2004).

We here study these strong effects of landmark and target blanking in several experiments. We vary the blanking and displacement times of two objects to investigate the specific criteria of the visual system when to accept the 'null hypothesis' of space constancy, and when to signal object displacement. In all of our experiments, initially two identical stimuli are presented, at about 6° in the visual periphery. In the first two experiments (Experiment 1A and B) participants perform a saccade to the stimuli which are moved and/or blanked during the saccade, and are asked to indicate which of both objects had moved. The findings confirm the strong landmark effects reported by, e.g., Deubel (2004) and specify the temporal conditions under which they occur. In two further experiments (Experiment 2A and B) we then investigate whether a saccade is indeed necessary to elicit the landmark-induced illusions of perceived displacement, or whether these effects also occur without eye movements. Indeed, in natural life objects are also sometimes temporally excluded from vision, e.g. due to moving occluders, and we should have mechanisms that are able to detect a possible displacement of the objects after occlusion. Therefore, we study these landmark effects also during gaze fixation. Similar to the results presented by Higgins and Wang (2010), we find that landmarks effects also occur for localization during fixation, with comparable spatial and temporal characteristics. This suggests that similar mechanisms that rely on stable spatial references affect localization both during fixation and saccades. Preliminary results from the study were reported at the European Conference on Eye Movements, Bern, 2005.

2. Experiment 1A

A first aim of the present study was to quantitatively measure the dynamics of events related to visual space constancy across saccadic eye movements. For this purpose we varied the delay between the post-saccadic presentations of two objects to determine the point of time where one object served as a landmark for post-saccadic localization. As soon as one object serves as a spatial reference, it should appear not to have been displaced during a saccade. Further, post-saccadic relocalization of another object should depend not only on its own transsaccadic displacement but also on the transsaccadic displacement of the landmark object.

A second question that we pursued was whether there exists a landmark effect also when *both* objects are presented with a blanking interval after the saccade. Earlier experiments had shown that displacement detection abruptly increased in a one-stimulus array with only a short blanking interval of 50–300 ms (Deubel et al., 1996). Therefore, the question arose: Would a blanking of both objects in a two-stimulus array prevent a landmark effect because the displacement of the first-reappearing object becomes visible?

2.1. Methods

2.1.1. Observers

Seven paid observers (six female, one male) participated in Experiment 1A. All reported vision that was normal or corrected to normal by contact lenses. Their age ranged from 23 to 28 years with a mean of 25. All were naive with respect to the aim of the study, but were experienced with the laboratory equipment from other eye movement related tasks. All experiments were done with the understanding and written consent of each participant, and conformed to the Declaration of Helsinki.

2.1.2. Apparatus

In this and all subsequent experiments the stimuli were presented on a 21 in. video-monitor at a frame rate of 100 Hz. The experiments were performed in a semi-darkened room; screen background luminance was 2.2 cd/m^2; the luminance of all presented stimuli was 25 cd/m^2. The observers viewed binocularly from a distance of 80 cm. Head movements were restricted by a chin and forehead rest. Eye movements were measured with a SRI Generation 5.5 Purkinje-image eye tracker (Crane & Steele, 1985) and sampled at a rate of 400 Hz. By digital differentiation of the sampled eye position signals, the computer derived a trigger signal indicating saccade onset. The saccade trigger was adjusted at a velocity threshold of 30 deg/sec such that stimulus modifications occurred before the eye reached maximum velocity.

2.1.3. Procedure

Each block contained 144 trials and was repeated 12 times with each observer in three separate sessions. As shown in Fig. 1 (left column) the observers initially fixated a small cross. After a random delay of 500–1100 ms the fixation cross disappeared and two small vertically aligned stimulus objects (crosses) appeared simultaneously 6° left or right of the fixation cross. Observers were instructed to saccade as fast as possible to the space between these two crosses. There was no differentiation between the objects such as target and distracter. Both objects had the same size (0.36°); the vertical spacing between the centers of the crosses was ±0.55° from the horizontal meridian.

Half of the trials in each block were 'no blank' trials (*Blank* = 0 ms), the other half were 'blank' trials (*Blank* = 200 ms). In the 'no blank' condition, one object (the 'upper' or the 'lower' object) disappeared with saccade onset for a variable time interval, while the other object was continuously present. The stimulus onset asynchrony (SOA), i.e., the time interval between saccade trigger and the reappearance of the blanked object, could be 0, 20, 40, 70 or 100 ms. Moreover, one of the two objects (the 'upper' or the 'lower' object) was displaced. The displacement could concern either the continuously present object (condition 'first moved') or the

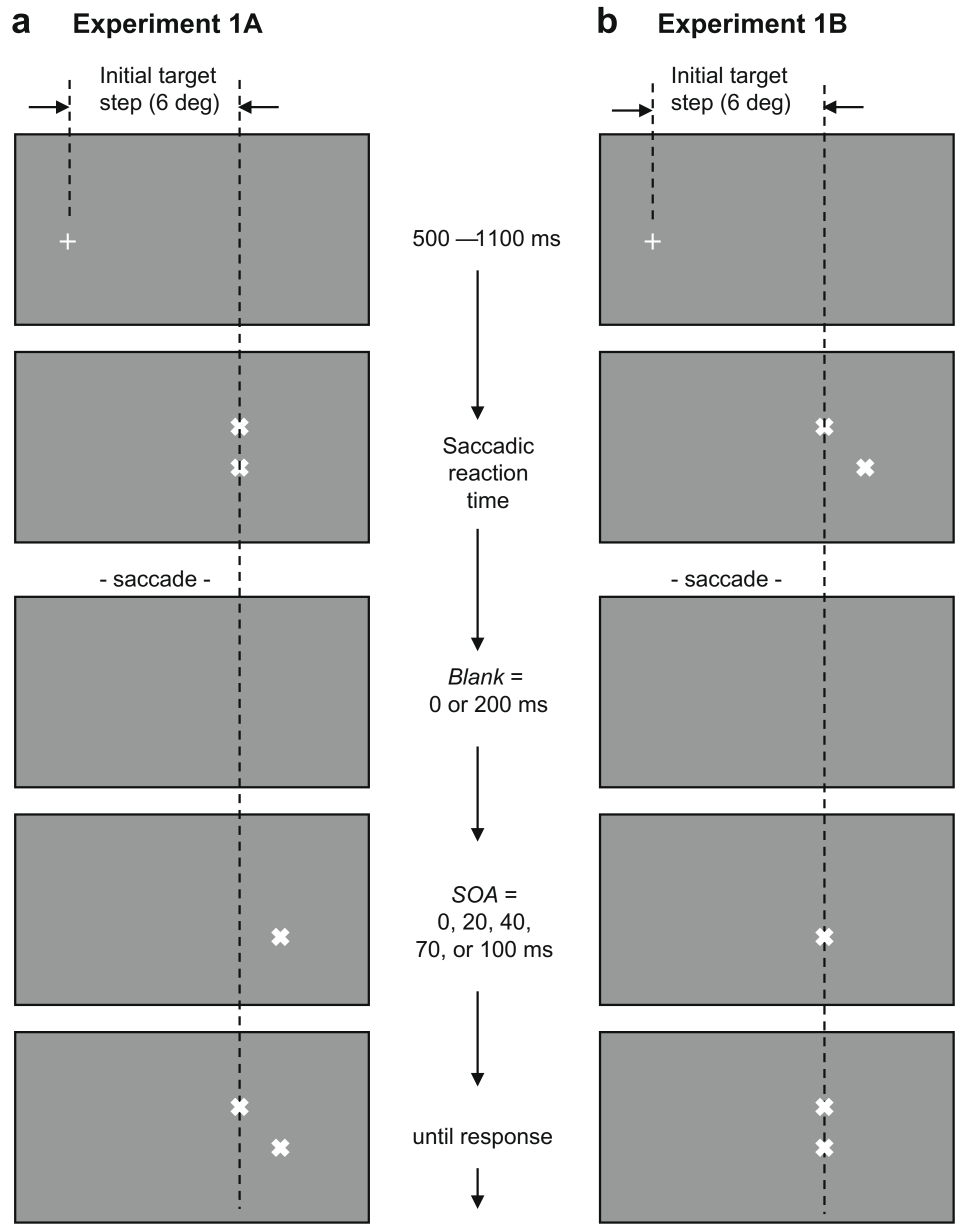

Fig. 1. Left: Stimulus sequences for a trial from Experiment 1A. Each trial started with a fixation cross (+). After a random delay of 500–1100 ms, the cross extinguished and two identical objects (×) appeared left or right by 6°. The observers were instructed to saccade into the space between the objects. With the onset of the saccade in the 'no blank' condition one object was blanked for 0, 20, 40, 70 or 100 ms while the other was continuously present. In the 'blank' condition both objects were blanked with saccadic onset for 200 ms. Then both objects appeared again, but with the same asynchronies as in the 'no blank' condition. During each trial one of the objects was displaced horizontally ±1°, either in the same or opposite direction as the saccade. Right: Stimulus sequence for a trial from Experiment 1B. Sequence of events is similar to Experiment 1A except that the pair of stimuli appeared with a horizontal offset before the saccade and ended vertically aligned after the saccade.

temporarily blanked object (condition 'second moved'). The displacement size was +1° ('onward') or −1° ('backward') with respect to the saccade direction. For illustration, the example shown in Fig. 1a depicts a condition where the continuously present object moved, while the blanked object reappeared after a delay at its previous position (condition 'first moved'). The zero time interval (SOA = 0) was a control condition, where we determined the detectability of displacement of one of the two continuously present objects during saccadic eye movements. In contrast, a SOA of 70 ms for example, could be described as an absence of one of the objects for 70 ms while the other was continuously present. In this case, we anticipated that the continuously present object would appear stable as a result of the landmark effect. Correspondingly, we expected an increased selection of the blanked object as appearing displaced.

In the 'blank' condition, both objects were removed with saccade onset for the blank interval of 200 ms. Then, the sequence of events was similar to the 'no blank' condition: one object reappeared, and the other followed after the already mentioned SOA of 0, 20, 40, 70, or 100 ms. For example, if one of the objects in the 'blank' condition was presented after a SOA of 40 ms the first object appeared at 200 ms and the other at 240 ms after saccade onset. Also, when the objects reappeared, one of the objects was displaced by +1° ('onward') or −1° ('backward') with respect to the saccade direction. The displacement could concern either the first presented object (condition 'first moved') or the object reappearing after the additional SOA (condition 'second moved').

As in the 'no blank' condition, the zero SOA served as control. Here both objects reappeared simultaneously after 200 ms. In consideration of the blanking effect, we expected an increase of the detection rate for both objects (Deubel et al., 1996). If transsaccadic spatial information becomes available through the blanking effect, none of the SOA conditions should further improve the detection rate. Furthermore, we expected that the first presented object should not become a reference object for the relocalization of the second presented object.

At the end of each trial, in a two-alternative forced choice, the observers‘ task was to report via button press which of the two objects (‘upper’ vs. ‘lower’) had moved, regardless of whether it moved onward or backward. The next trial started with a new fixation cross at the middle position between the peripheral objects.

Because in this experiment our main interest was to analyze the temporal aspects of building up a spatial reference, differences in the displacement detection rate depending on either the displacement direction with respect to the saccade direction (‘onward’ vs. ‘backward’) or the spatial position (‘upper’ vs. ‘lower’) were unimportant. It was therefore sufficient to compare the displacement detection rates of the first and the second presented objects. As soon as one object served as a landmark for the post-saccadic localization of the other, the detection rate of the landmark object should get worse – it would always tend to be perceived as stable as a result of the ‘null hypothesis’. The second presented object would be perceived as moved because of the discrepancy between the pre-saccadic and the post-saccadic information about the relative position of that object. Accordingly, the displacement detection rate of a landmark object should degrade while the displacement detection rate of the other object should improve.

For statistical analysis we used a three factor design ($2 \times 2 \times 4$) with the variables BLANK (‘no blank’ and ‘blank’), MOVE (‘first moved’ and ‘second moved’) and SOA (20, 40, 70 and 100 ms). Further, there were the two control conditions for the BLANK (‘no blank’ and ‘blank’) where the SOA was 0 ms.

2.2. Results

Trials in which the eyetracker lost track of the eye were excluded from subsequent analyses as well as trials with oculomotor response latencies below 100 ms and above 900 ms (3.2%).

Saccadic amplitude was independent of motion of an object in the saccade direction or in the opposite direction (mean 5.56°). It was also independent of whether the trial was a blank or a no blank control trial. This confirms the automatism of saccadic eye movements, which cannot be modified after their onset. The latency of the first saccade was also independent of the trial condition; mean latency was 205 ms.

Before we pooled the data of saccade-relative displacement directions (‘onward’ and ‘backward’) as well as of the two positions (‘upper’ and ‘lower’), we analyzed their effect on the displacement detection rate. As in earlier experiments (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Deubel et al., 1996) we found a significantly better detection rate for displacements in the direction of the saccade (“onward”) than against the saccade eye movement direction (“backward”), independent of the presentation condition [$t = 4.07$, df = 6, $p < 0.01$], as if there were a slight underconstancy in our sparse environment. The higher detection rate was presumably connected with undershoots of the primary saccade. The absolute error between the eye position after the primary saccade and the new position of the displaced object increases with undershoots and therefore allowed a better detection rate for displacements in the eye movement direction.

There was also a significant difference in the detection rate depending on the position of the displaced object [$t = 2.76$, df = 6, $p < 0.05$]. Displacements of the lower object were perceived better in all conditions than displacements of the upper object, a fact that could not be explained by the eye movements. As a result of the center-of-gravity effect (Findlay, 1982), all primary saccades ended in the space between the two crosses (mean vertical deviation 0.07°). In 37% of all trials there was no second or corrective saccade. In the remaining trials, the second saccade tended in the direction of the first presented object (up or down) [$t = 4.12$, df = 6, $p < 0.01$]. The tendency was symmetrical in both directions about the center line, but the amplitude was too small for direct fixation of the object.

In a repeated measures ANOVA we analyzed the latency of the second saccade with a two-way within-observer 2×5 design with the factors BLANK (‘no blank’ and ‘blank’) and SOA (0, 20, 40, 70 and 100 ms). The ANOVA revealed significant main effects for BLANK [$F(1, 6) = 995.43$; $p < 0.001$] and SOA [$F(4, 24) = 12.58$; $p < 0.001$]. In the ‘no blank’ condition the mean latency was 309 ms with respect to the end of the first saccade, in comparison to the ‘blank’ condition, 456 ms. These long latencies as well as the fact that there was no interaction between the factors SOA and BLANK [$F(4, 24) = 0.53$; $p > 0.7$] indicate that the second saccade was initiated after both objects reappeared.

As already mentioned, because we were interested primarily in the relative detection rates as a function of blank durations, we pooled the data and differentiated the displacement detection rates only between the variables BLANK (‘no blank’ or ‘blank’), MOVE (‘first moved’ or ‘second moved’), and SOA.

Fig 2a and b present the percentage of correct indication of the moved target as a function of the variables MOVE and SOA. Fig. 2a depicts the data from the ‘no blank’ conditions, Fig. 2b those of the ‘blank’ condition. The accuracy for displacements in the control conditions (SOA = 0 ms) was used as a baseline for the detection rate: As expected, displacement detection was significantly better in the ‘blank’ condition (87%) than in the ‘no blank’ condition (76%) [$t = -4.72$, df = 6, $p < 0.01$]. This effect supported our earlier finding that blanking breaks the perceived stability of an object as a result of the ‘null hypothesis’ and the pre-saccadic information becomes available. Since saccade duration averaged 34 ms, a SOA of 20 ms in the ‘no blank’ condition could be described as an off- and onset of a stimulus occurring during the saccade. Therefore, at the end of the eye movement both objects were already present for this SOA, and therefore we found nearly the same detection rate as in the control condition.

For larger SOAs in the ‘no blank’ condition there was only one stimulus present at the end of the saccade, while the other reappeared after a variable delay. As can be seen in Fig. 2a, this resulted in a prominent bias to perceive the first present stimulus (i.e., the continuously present object) as stable, and to attribute motion to the second present stimulus. As a consequence, the detection rate of the ‘first moved’ object decreased rapidly whereas the rate of the ‘second moved’ object increased. Obviously, the asynchronous stimulus presentation led to a strong illusion: already for a SOA of 70 ms displacements of the continuously present object were correctly perceived in only 14% of all trials, and mostly attributed to the other, blanked object (Fig. 2a, dashed curve). This implies that the continuously present stimulus was taken as a reference object for the relocalization of the second presented stimulus – the perceived movement results from an adjustment relative to this first presented object. Because the pre-saccadic information about the spatial range between the two objects does not fit with the post-saccadic information, the visual system assumes that the second presented object must be the moved one.

Contrary to our expectation, similar effects were found in the ‘blank’ conditions, reflected in a bias towards perceiving the object presented first after the 200 ms blanking period as stable (Fig. 2b). However, in these conditions the induced effect was somewhat weaker, and resulted for longer SOAs in a detection accuracy of about 40%, so that 60% of the displacements of the first presented stimulus were misattributed to the delayed stimulus.

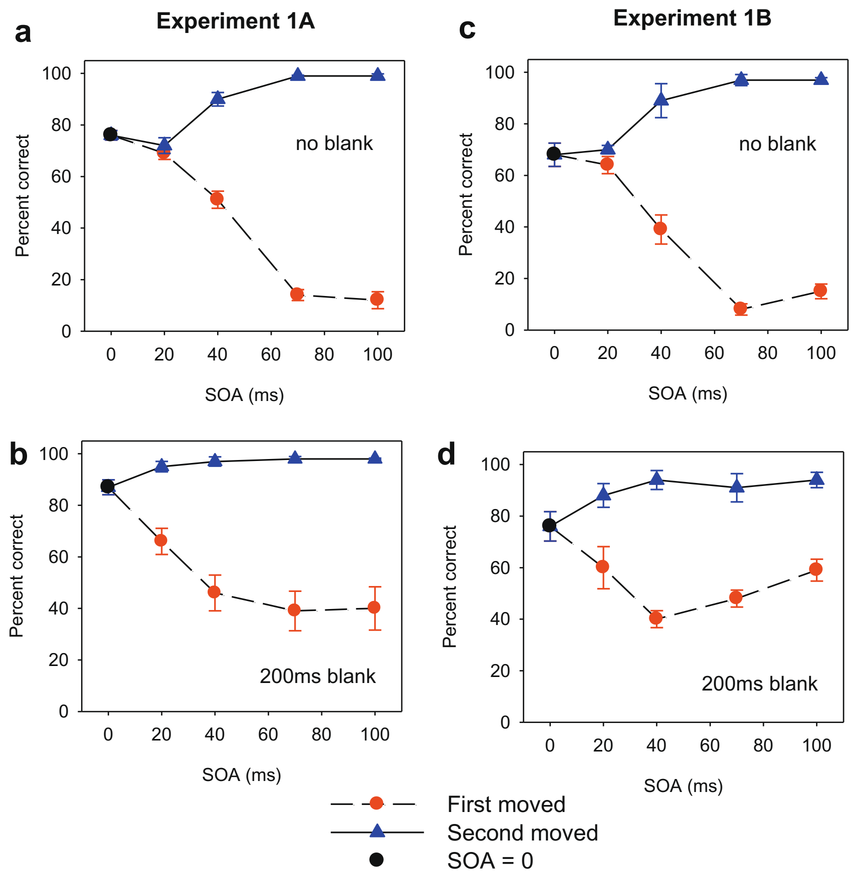

Fig. 2. Detection rates in percent perceived correct for different SOAs following saccadic eye movement onset. Error bars indicated standard error of the mean. (a and b): Data from Experiment 1A. (c and d): Data from Experiment 1B. Upper graphs: The 'no blank' condition. Lower graphs: 'blank' condition. The baseline detection rate is given at 0 SOA ($t = 0$ ms) for both conditions, where both objects appear simultaneously. The dashed curves represent the data from trials in which the continuously present/first presented object underwent a displacement; the solid curves those where the second presented object was displaced.

These findings were confirmed by statistical analyses. In the $(2 \times 2 \times 4)$ repeated measure ANOVA described above we analyzed the detection rates for the displaced objects. The object shown with a delay (second moved) was judged to be the displaced one significantly more often than the first-moved one, reflected in a significant main effect of the variable MOVE [$F(1, 6) = 269.67$; $p < 0.001$]. The difference in accuracy between these two conditions increased with SOA [$F(3, 18) = 56.16$; $p < 0.001$], and there was also an interaction between MOVE and SOA [$F(3, 60) = 75.80$; $p < 0.001$]. The variable BLANK ('no blank' vs. 'blank') showed a smaller but significant main effect [$F(1, 6) = 9.96$; $p < 0.05$], indicating that due to the blanking the visual system was able to use some stored information about the pre-saccadic localization (the 'blanking effect', Deubel et al., 1996). Further, there was no significant interaction between the two factors BLANK and MOVE [$F(1, 60) = 2.28$; $p > 0.15$], indicating that in both conditions ('no blank' and 'blank') the first presented object becomes the reference object. However, there was an interaction between the BLANK conditions and SOA indicating stronger effects of the increasing SOA in the 'no blank' condition [$F(3, 60) = 3.08$; $p < 0.05$]. Finally, the three-way interaction of BLANK $\times$ SOA $\times$ MOVE was significant [$F(3, 60) = 19.32$; $p < 0.001$].

2.3. Discussion

The experiment demonstrated that landmarks are highly efficient determinants for the perception of stability, or of object displacement across saccadic eye movements. This is in line with previous findings of Deubel (2004). We found a strong illusion effect with a blanking of only one stimulus as well as with a blanking of both stimuli, in that the first present object that is found after saccade completion tended to be seen as stable, regardless of which object had actually been displaced. The strength of the motion bias depended on the delay in presentation between the objects. It is particularly surprising that even a very short delay in presentation was sufficient for eliciting a strong motion sensation. So, since on average the saccade ended about 25 ms after the saccade trigger signal, the unmoved stimulus presented with an SOA of 40 ms reappeared only about 15 ms after the eyes had stopped, nevertheless, this short asynchrony was sufficient to decrease detection accuracy to only 51% (Fig. 2a, dashed curve). The illusion effect reached its maximum with a delay in object reappearance of about 45 ms after the eye movement was finished (i.e., for a SOA of 70 ms). Thereafter, the effect seemed to remain constant.

If there was a blanking of equal duration of both objects that was longer than the duration of the saccade (200 ms 'blank' condition), the visual system was able to use information about the pre-saccadic location of both objects, which reflects a blanking effect as previously described by Deubel et al. (1996). But the availability of this pre-saccadic information decreases abruptly with an asynchrony in presentation between the two objects. Paradoxically, in the blanking conditions the first-reappearing object's displacement would have been easily detected if it were the only object in the visual field (Deubel et al., 1996). The presence of a second object blanked for a longer time, however, prevents the displacement from being perceived, and the motion is assigned to the second-appearing object.

The results show that perceptual stability is not only determined by an extra-retinal signal but also by the object that is found when the eyes land – this object serves as a spatial reference. The blanked object is then seen as displaced because its position is judged relative to the landmark, whose position is assumed to be stable. Thus, a 'null hypothesis' of space constancy for continuously available objects was confirmed: observers avoided assigning the displacement to a continuously presented object, both before and after saccades. The existence of reference objects in a blanking paradigm cannot be explained in terms of compression of space (e.g., Lappe, Awater, & Krekelberg, 2000; Matsumiya & Uchikawa, 2003) because the saccadic eye movement was – in most of the experimental conditions – already finished when judgments were made.

Detection of displacement was generally better in the lower visual field, an effect which is not explained in the current context but which has been observed by Gysen, Verfaillie, and DeGraef (2002a) in the context of perisaccadic target motions. Previc (1998) argues that the sensorimotor branch of the visual system is ecologically biased toward the lower visual field. In our context, this would mean that our task engages primarily mechanisms related to eye movement and spatial processing, as opposed to the pattern-recognition functions of the cognitive system. Could stationary visible landmarks due to the ambient lighting condition, such as the borders of the monitor, have contributed to the results? We think that this is unlikely, since Deubel (2004) has shown that even high-contrast peripheral borders contribute only little to the landmark effect.

3. Experiment 1B

We hypothesized that the effects in Experiment 1A arose because the first-reappearing object served as a reference object for the second one. The first-appearing target and the second-appearing target reappear after the saccade with a horizontal offset, however. This might result in a low-level apparent motion signal with a component in or against the direction of the saccade, biasing the detection of displacement. To determine whether the illusions we found in Experiment 1A arose as a result of this apparent motion sensation, we ran a control experiment in which the pair of stimuli appeared with a horizontal offset before the saccade and ended vertically aligned after the saccade (Fig. 1b). Any bias resulting from apparent motion should then be vertical and should therefore not affect the judgment of horizontal displacement. If we find the same pattern of displacement detections as in the main experiment, we would be sure that the decreased detection rate of the first presented object arises from a landmark effect rather than from apparent motion.

3.1. Methods

3.1.1. Observers

Three paid observers ranged in age from 23 to 28 years with a mean of 26 years. All were naive with respect to the aim of this study, but had run in at least one of the other experiments.

3.1.2. Procedure

The procedure and the trial conditions of the two experiments were analogous to those in Experiment 1A, except that the spatial configuration of the stimuli differed. Here, the two crosses were first presented with a horizontal offset, 6° and 7° left or right so that after the displacement they were vertically aligned. Because at the end of each trial the observer had to decide which object was horizontally displaced, we assumed that the vertical alignment of the crosses as well as the constant distance of 6° to the initial fixation cross were neutral with respect to horizontal displacement and did not support the detection of horizontal movements of an object under our conditions.

The experiment was designed like Experiment 1A with three main factors ($2 \times 2 \times 4$): BLANK ('no blank' and 'blank'), MOVE ('first moved' and 'second moved') and SOA (20, 40, 70 and 100 ms), and a control condition (SOA = 0) where both objects were presented simultaneously with or without a blank.

3.2. Results and discussion

The accuracy of displacement detection as a function of presentation conditions is shown in Fig. 2c and d. As in Experiment 1A the displacement detection rate of the first present stimulus decreased with an increasing SOA for both of the conditions 'no blank' and 'blank'. The repeated measures ANOVA showed a significant main effect of the factor MOVE ('first moved' and 'second moved') [$F(1, 2) = 280.11$; $p < 0.01$]. Probably because of the limited number of observers and the differences in their individual performance, the other factors produced no significant main effects; BLANK ('no blank' and 'blank') [$F(1, 2) = 13.41$; $p > 0.067$] and SOA (20, 40, 70 and 100 ms) [$F(3, 6) = 1.26$; $p > 0.35$]. Nevertheless the strength of the perceived displacement sensation depended on all three factors. All possible interactions between the three factors were significant: BLANK × MOVE [$F(1, 20) = 21.51$; $p < 0.001$], SOA × MOVE [$F(3, 20) = 29.50$; $p < 0.001$], BLANK × SOA [$F(3, 20) = 4.50$; $p < 0.05$] and BLANK × SOA × MOVE [$F(3, 20) = 25.87$; $p < 0.001$]. Statistically, a large number of significant interactions can mask a main effect.

The similarity of results in Experiment 1A with post-saccadically misaligned stimuli and Experiment 1B with post-saccadically aligned stimuli indicates that the alignment variable was not critical. The timing of the respective appearances and disappearances of the two stimuli dominated the results in both cases.

4. Experiment 2A[1]

The 'null hypothesis' and the building up of reference objects have always been associated with saccadic eye movements. To test whether this assumption is true or whether the visual system has a general strategy to maintain space constancy, we ran additional experiments similar to Experiment 1A and B except that observers now maintained fixation. During fixation, displacements of continuously presented objects beyond a very small threshold are normally detected without error. If two objects are blanked and one of them is displaced, but one reappears before the other, the first-reappearing object might be taken as a landmark, and displacement be assigned to the other object regardless of which one was actually displaced.

4.1. Methods

4.1.1. Observers

Seven paid observers (six female, one male) participated in this experiment. All reported normal vision or vision corrected to normal by contact lenses. Their age ranged from 22 to 25 years with a mean of 24 years. All observers were naive with respect to the aim of the study, but were experienced with the equipment from other eye movement related tasks.

4.1.2. Procedure

Each block contained 144 trials and was repeated six times with each observer in two separate sessions. The stimulus sequence was similar to Experiment 1A with the exception that a fixation cross had to be fixated during the whole trial, and that the saccadic

[1] A demonstration of the stimuli of Experiment 2 can viewed at: http://www.paed.uni-muenchen.de/~deubel/References_in_fixation_demo.html.

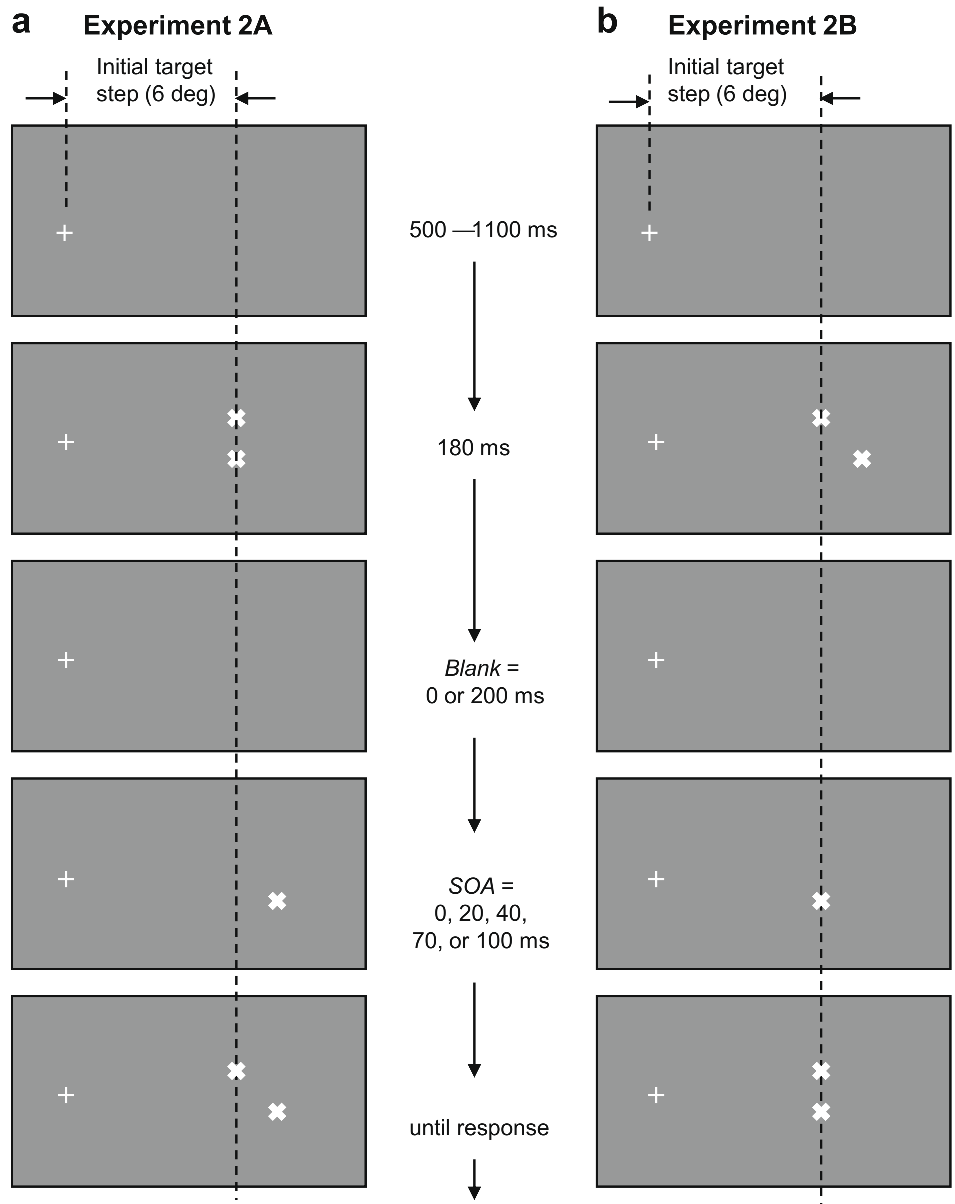

Fig. 3. Stimulus sequences for trials from the fixation Experiments 2A and B.

reaction time was replaced by a constant time interval of 180 ms (see Fig. 3a).

At the end of each trial, in a two-alternative forced choice, the observers reported which of the objects ('upper' vs. 'lower') had moved, regardless of movement direction. To prevent a cue from constant visual directions, the next trial started with a new fixation cross between the two peripheral objects.

4.2. Results

Trials with signal loss of the eye tracker due to blinks were excluded from subsequent analyses, as well as trials in which the observer elicited a saccade in any direction (4.1%).

The data showed the same difference in the detection rate depending on displacement direction as in Experiment 1A. Again, 'onward' displacements were better detected over all conditions than 'backward' displacements [$t = -3.90$, df = 6, $p < 0.01$]. Thus, the previous assumption that the better detection rate is due to undershoots of saccadic eye movements was not supported. The independence from eye movements argues for a general better performance of the visual system in this movement direction, rather than a saccade-related recalibration.

A paired t-test showed no significant difference between detection rate of upper and lower objects [$t = -2.15$, df = 6, $p = 0.075$]. Based on the same reasoning as in Experiment 1A, we pooled both displacement directions ('onward' and 'backward') as well as the two positions of the moved object ('upper' and 'lower'), and only differentiated between the 'first moved' and 'second moved' object.

The results displayed in Fig. 4a show that displacement detection was perfect (99% correct) in the control condition when both objects were continuously present ('no blank' and SOA = 0 ms). In contrast to the saccadic eye movement condition, a blanking of equal magnitude of both stimuli during fixation reduced the displacement detection rate significantly to only 73% [$t = 8.01$, df = 6, $p < 0.001$], see Fig. 4b.

For further analyses we again used a repeated measures ANOVA with a within-observer design ($2 \times 2 \times 4$) and the factors BLANK

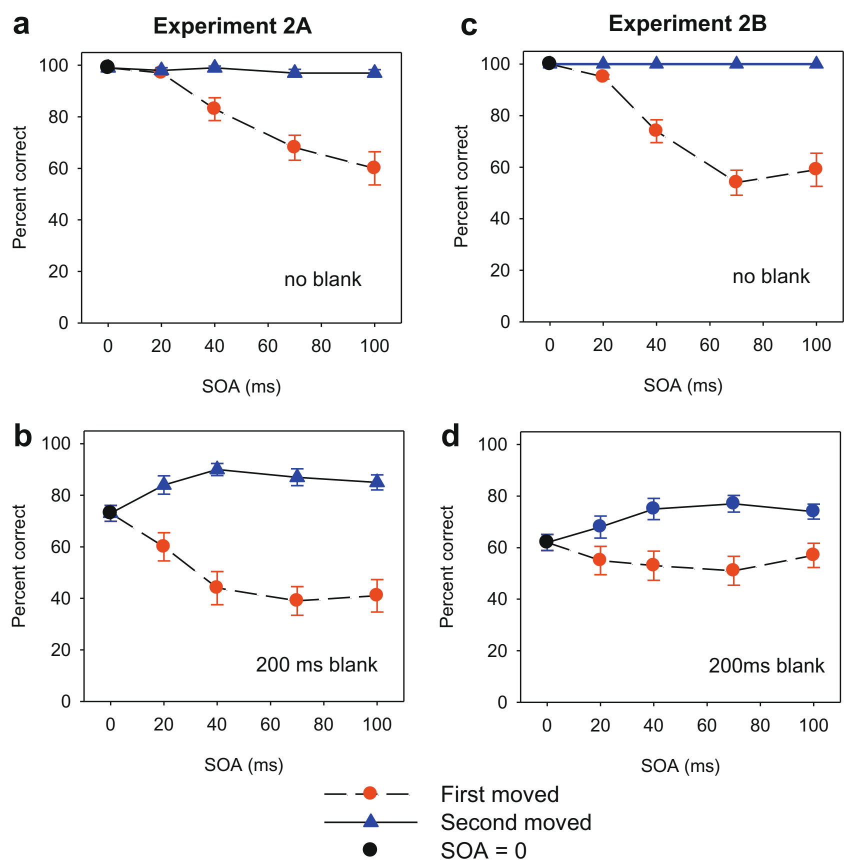

Fig. 4. Results from Experiments 2A and B (Fixation experiments).

('no blank' vs. 'blank'), MOVE ('first moved' vs. 'second moved') and SOA (20, 40, 70 and 100 ms).

Because the 200 ms blank in presentation reduced the detection rate of displacements in all conditions, the ANOVA revealed a significant main effect of the factor BLANK [$F(1,6) = 162.16$; $p < 0.001$]. Further, the main effect for MOVE was significant [$F(1,6) = 85.78$; $p < 0.001$], reflecting the fact that displacement detection for the continuously or first present object deteriorated for longer SOAs. In particular, in the 'no blank' condition this was unexpected during fixation where normally even very small displacements can be easily detected (see, e.g., Fig. 7a in Deubel et al., 1996). However, in this experiment an off- and onset of the unmoved stimulus produced a decrease of the displacement detection rate of the continuously presented, but displaced object nearly to chance level (~60%). It seems that the offset or the onset of the other object attracted attention, so that observers were unable to perceive the displacement of the continuously presented object. This result implies that the 'null hypothesis' of the visual system that the world is stable applies not only to saccadic eye movements but also to all unattended objects during fixation. The detection rate of the second presented object in the 'no blank' condition remained perfect for all SOAs.

In the condition including the 200 ms blank, a delay in the presentation between the two objects led to a further decrease in the displacement detection rate when the first presented object moved, whereas displacement detection rate of second presented object increased. This fact supported evidence that the asynchronous presentation aroused an additional displacement sensation for the blanked (but unmoved) object. The resulting illusion strengthened with the delay in presentation, as confirmed by a significant main effect for SOA [$F(3,18) = 18.42$; $p < 0.001$].

All interactions between the three within-observer variables were significant. The interaction BLANK $\times$ MOVE [$F(1,60) = 67.59$; $p < 0.001$] could be explained by the fact that the detection difference between the 'first moved' and 'second moved' trials was larger in the 'no blank' condition. The same holds on for the interaction between BLANK $\times$ SOA [$F(3,60) = 3.88$; $p < 0.05$], where we found a stronger effect of increasing SOA on accuracy in the 'no blank' conditions. Also, with a longer SOA, the effectiveness of the illusion produced by the non-delayed object increased. Statistically, this was confirmed by the interaction between MOVE $\times$ SOA [$F(6,60) = 30.48$; $p < 0.001$].

To summarize, we found similar illusion effects as in Experiment 1A. When the two objects disappeared and reappeared after a 200 ms blank during fixation, there was a strong tendency to perceive the first presented object as stable, and to attribute displacement to the second presented object. The illusion even occurred, although to a weaker degree, with a temporary blanking of only one stimulus, and the other being continuously present. As in the saccade conditions of Experiment 1A, the strength of the illusion depended on the delay in presentation between the objects. This fact was confirmed by the significant three-way interaction of BLANK $\times$ MOVE $\times$ SOA [$F(3,60) = 4.39$; $p < 0.01$].

4.3. Discussion

The blanking illusion is a tendency to assign displacement to a temporarily blanked target, in the presence of a non-blanked target, regardless of which actually moved. We had assumed that the illusion arose as a result of the 'null hypothesis' of space constancy coupled to saccadic eye movements. Thus we were surprised that the illusion also occurred during fixation. We explain this through the initial presence of an object that establishes a spatial context; the position and displacement of a subsequently seen object, in our experiment the one blanked for a longer time, are interpreted in the context of an already-established spatial anchor. In the saccade context this can be interpreted as the 'null hypothesis' that the world is stable, but we find here that the principle applies more broadly.

It is interesting to note that in the fixation condition, the introduction of the 200 ms blank interval leads to a remarkable deterioration of displacement detection. For SOA = 0 for instance, performance is perfect in the "no blank" condition but is reduced to 73% in the "blank" condition (cf. Fig 4a and b). This is in line with a similar finding by Deubel et al. (1996, Experiment 5) and indicates that displacement discrimination during fixation may be based on two different mechanisms: In the 'no blank' condition, sensitive low-level motion detectors allow for the discrimination of even very small displacements. For the 200 ms blanking, however, these motion signals become unavailable, and displacement detection has to rely on a comparison of a short-term memory representation of the initial target location with the target location reappearing after the blank.

In this experiment, the delayed appearance of the second object may have aroused an apparent motion sensation with a component away from the onset of the first object. As a result of this apparent motion, observers may have perceived the second stimulus, with an increased presentation delay, as the stimulus that moved. Testing this hypothesis is the goal of the control Experiment 2B in which both stimuli were finally vertically aligned objects.

5. Experiment 2B

5.1. Methods

5.1.1. Observers

The same three observers who were run in Experiment 1B also participated in this experiment.

5.1.2. Procedure

The procedure and trial conditions were analogous to those in Experiment 1B, except that the observers had to fixate during each trial and the saccadic reaction tine was replaced by a constant delay of 180 ms. The two crosses were first presented 6° and 7° left or right so that after the displacement they were vertically aligned at 6° eccentricity (Fig. 3b). Because at the end of each trial the observer had to decide which object was horizontally displaced, we assumed that the vertical alignment of the crosses as well as the constant distance of 6° to the initial fixation cross were neutral and did not support the detection of horizontal movements of an object under our conditions.

5.2. Results and discussion

Basically, we found a very similar pattern of displacement detection as in Experiment 2A (see Fig. 4c and d). A repeated measures ANOVA showed a significant main effect of all three factors: MOVE ('first moved' and 'second moved') [$F(1,2) = 49.7$; $p < 0.001$), BLANK ('no blank' and 'blank') [$F(1,2) = 136.01$; $p > 0.01$] and SOA (20, 40, 70 and 100 ms) [$F(3,6) = 6.39$; $p > 0.01$]. The limited number of observers and their large individual differences in detection rate caused the results of the interactions between the three factors to be less clear than in Experiment 1; BLANK × MOVE [$F(3,20) = 4.73$; $p < 0.05$], SOA × MOVE [$F(1,20) = 3.58$; $p = 0.07$] and BLANK × SOA [$F(3,20) = 4.18$; $p < 0.05$]. The three-way-interaction BLANK × SOA × MOVE was not significant [$F(3,20) = 2.08$; $p > 0.1$].

Since we found the same pattern of displacement detection as in Experiment 2A, we conclude that low-level apparent motion due to the final relative position of the two stimuli is not responsible for the motion sensation. If there was any apparent motion in this experiment, it was primarily vertical, as two targets appeared vertically aligned but at different times. Nonetheless, the offset in appearance of the two objects affected the perception of left–right motion.

6. General discussion

6.1. The 'reference object' theory

We have exploited the 'blanking' effect (Deubel et al., 1996) to further define the characteristics and mechanisms of space constancy. In all of the experiments observers were worse in detecting displacements of continuously presented objects. The data are consistent with the hypothesis that the visual system assumes a 'null hypothesis' of position constancy for continuously available objects. The relocalization of objects presented with a delay after the eye movement depends on pre-saccadic information about the spatial relations between the two objects. As a result of this 'null hypothesis', the first presented stimulus became a spatial reference for a delayed object in the display.

By directly comparing a continuously available object with a blanked one, we show that the continuous object affects the localization of the blanked object, so that the blanked object is seen as moving, regardless of which object actually moved. The application of these phenomena to space constancy supports our previously described 'reference object theory' (Deubel & Schneider, 1994; Deubel et al., 1996) which assumes that after a saccadic goal has been selected, information about particular features and relational information from objects near the target are stored in transsaccadic memory for later re-identification. At the end of an eye movement, the visual system searches for conformities between the memory representation and the image information within a limited region. If the saccadic target is identified, the spatial relations are matched. If no target is found, but other objects can be recognized, visual stability is maintained because the visual system assumes that their positions do not change during saccadic eye movements.

New to this study is the finding that the benefit of blanking for displacement detection extends also to situations where both objects are blanked (200 ms 'blank' condition). Even if it too is blanked, the first object to appear becomes a landmark for the other. Only if neither object has a timing advantage does the landmark search fail, and either object is likely to be seen as moving. As soon as one object has the advantage of appearing first, the visual system seizes on that object as the spatial reference.

Higgins, Irwin, Wang, and Thomas (2009) and Higgins and Wang (2010) have argued that the "blanking effect" (i.e., the improvement of displacement detection due to the blanking of the target after the saccade) and the "landmark effect" (Deubel, 2004) are related to different mechanisms. Our present finding supports this view showing a clear dissociation: While landmark effects exist in both saccade and fixation conditions, target blanking *improves* displacement detection in the saccade conditions, but *impairs* performance in the fixation conditions. This suggests that the effects of blanking are specific to the occurrence of a saccade (or a blink, see Higgins et al., 2009), while the landmark effect is based on more general mechanisms subserving perceptual stability.

6.2. Similar processing during saccades and fixation

A central and unexpected result of our study is that we obtained the same pattern of displacement rates in both saccade and fixation conditions, though the effects were somewhat weaker in the fixation conditions. Also dynamically, the emergence of the landmark effect with increasing SOAs was surprisingly similar for saccades and for fixation. Moreover, information about the pre-saccadic target location, which was available through a blank in a presentation during and after saccadic eye movements, did not prevent a strong illusion effect. Therefore, it seems that the visual system has an overall strategy to maintain space constancy on the basis of the location of the first available object after a saccade, or the first-restored item during fixation. Generally, the built-in assumption or 'null hypothesis' holds for space constancy, a 'first come, first served' rule. As a result of this rule, the first presented object was seen as stable in both saccade and fixation experiments.

The findings suggest that the mechanisms previously thought to apply uniquely to space constancy across saccadic eye movements also apply to conditions of constant fixation. During fixation, we have found a continuously present object more likely to be perceived as not moving than a blanked object. Consequently we can link the space constancy 'null hypothesis' to conditions of normal vision during fixation. The mechanisms that facilitate space constancy continue to function during fixation.

Although there is no saccade in the fixation condition, there is an attention shift to the new location of the stimulus objects. We would like to speculate that it is the attention shift that normally accompanies a saccade, rather than the eye movement itself, that is decisive in eliciting the blanking and stability effects that we have demonstrated. Indeed it has been suggested that attention shifts are accompanied by recalibrations of represented space even in the absence of saccadic eye movements (Pisella & Mattingley, 2004). When a saccade is not accompanied by an attention shift, as in the fast phase of vestibular nystagmus, there is no space constancy (Dittler, 1921), but when there is an attention shift without a saccade, as in our 'fixation' conditions, brain mechanisms that normally facilitate space constancy become active. Thus, the attention shift may be sufficient, and the saccade may be not necessary, to obtain a landmark effect.

Experiments by others have shown results reinforcing this attention shift conception. Ostendorf, Fischer, Gaymard, and Ploner (2006) found mislocalization of targets flashed before or during saccadic eye movements, replicating phenomena originally observed by Matin and Pearce (1965), and found similar mislocalizations during saccades simulated by rapid motion of visual references. The effects on apparent positions began about 50 ms before the simulated saccades, just as they did before real saccades, and included both apparent shifts and apparent compression of space. While Ostendorf et al. (2006) took care to reproduce the dynamics of saccades in their target shifts during fixation, we have found that precise simulation of saccade dynamics is not necessary; a simple step displacement has the same effects.

In classical induced motion it is always a large object that induces an apparent motion in a smaller object (Duncker, 1929), without a common spatial displacement of the two objects that would induce a global attention shift. Our effects occurred even for small targets identical in size, and the perceived displacement or stability was determined by timing of disappearance and reappearance rather than by object size.

Our finding that landmarks effects are present also during fixation is perfectly in line with a recent study by Higgins and Wang (2010). These authors partially anticipated one of our conditions [fixation, blank, SOA = 100] with the result, consistent with our findings, that the object shown first is more often perceived as the stable one, regardless of which one actually moved. Our study is complementary to their findings in several respects: First, by studying both saccade and fixation conditions in a similar experimental procedure, the present results allow to compare the relative strengths of the landmark effects under both conditions. Further, Higgins and Wang studied the landmark effect with long blanking periods of 1200 ms. In contrast, we analyzed the time course of the landmark effect for shorter blanking and by systematic variation of SOA, and found that presentation asynchronies of only a few tens of milliseconds are already sufficient to produce a marked bias to assign displacement to the later shown objects. Surprisingly, our study revealed a landmark effect even for the continuously present object during fixation (Fig. 4a). Finally, while Higgins and Wang (2010) studied landmark effects in central vision, our stimuli appeared in the visual periphery. Taken together, the results of both studies demonstrate that the landmark effect in target localization is a robust finding, occurring over a variety of spatial and temporal conditions, both across saccades and during fixation.

6.3. Trans-saccadic memory and visual short-term memory

Our results also have implications for the nature of trans-saccadic memory, the information that is preserved across a saccade from one fixation to the next. If the rules of perception are the same for saccadic and fixation conditions, as we have found, then trans-saccadic memory and visual short-term memory (visual information that extends beyond retinotopic iconic memory) might have similar properties or even share the same mechanism, as previously proposed (Irwin, 1992). Indeed, relational information in trans-saccadic memory is maintained in a similar manner to that in visual short-term memory (Carlson-Radvansky, 1999). In both eye movement and fixation trials, same/different judgments were faster and more accurate when two successive patterns did not share structural relations. These relations take time to build up (Brenner, Meijer, & Cornelissen, 2005): when the targets are quick flashes at short intervals rather than continuously present (or briefly blanked) objects, their relative positions are almost exclusively determined by their respective retinal positions, whether or not a saccade changes eye orientation in the meantime. The same happens during smooth pursuit, where localization illusions increase systematically as target duration decreases (Rotman, Brenner, & Smeets, 2005).

While the visual-spatial comparison task required in the fixation experiments can be done based on a visual memory organized in retinotopic coordinates, the same task in the saccade condition must involve some non-retinotopic representation, such as by encoding pre-saccadic information in allocentric coordinates or by updating ("remapping") the memory representation based on the saccade. Indeed, we have previously proposed (Deubel, 2004; Deubel, Schneider, & Bridgeman, 2002) that transsaccadic integration involves the pre-saccadic encoding of the saccade target and some surrounding objects in a short-term visual memory that preserves spatial relations, but is not tied to retinotopic coordinates. After the saccade has landed on the new target, this relational information might be spatially anchored onto the visual reafference by means of the landmark information, and supported by extraretinal signals about eye position.

In conclusion, our findings suggest that the mechanisms that normally enable space constancy are part of the normal processing of spatial information by vision, and operate continuously both in the transsaccadic environment and in normal visual perception.

Acknowledgments

This work was supported by the Deutsche Forschungsgemeinschaft; Research Group FOR 480 (Project De 336/2). We thank Birgitt Aßfalg for her help in running the experiments.

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