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Perceived slant from Werner's illusion affects binocular saccadic eye movements

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We examined whether binocular saccadic eye movements are determined solely by disparity-defined slant or whether they are influenced by both disparity-defined and perceived slant. The Werner illusion was used to distinguish a plane's disparity-defined slant from its perceived slant. Three subjects viewed a horizontally elongated test strip that was flanked vertically by two planes. The perceived slant of the test strip depended on the slant of the flanking planes. Subjects estimated the perceived slant of the test strip by adjusting the angle between two lines in a symbolic top view. The saccadic eye movements between targets on the test strip were recorded both with visual feedback ("later saccades") and without visual feedback ("first saccades"). We calculated vergence differences for saccades between targets on the test strip (and for fixation on these targets). For each geometrical test strip slant we examined whether the vergence differences could be explained as an effect of perceived slant. This study shows that saccadic eye movements are determined predominantly by the disparity-defined slant, but they can be affected by perceived slant, particularly when multiple saccades are being made.

Keywords: binocular vision, saccades, slant perception, disconjugacy

Introduction

It is generally accepted that different aspects of visual information are processed in different areas of the brain. Ungerleider and Mishkin (1982) stated that the nonspatial qualities of an object are processed in the inferior temporal cortex, whereas its spatial location is processed in the posterior temporal cortex. Goodale and Milner (1992) reinvestigated this division and proposed the existence of action and perception pathways. In their view, the external information is represented twice, once (ventrally) for perception and once (dorsally) for action. As a consequence, there could be a dissociation between what animals and human beings perceive and how they act.

Many studies have attempted to prove or reject this dissociation using geometrical illusions. Illusions constitute an ideal tool for the study of this dissociation because they reflect differences between physical stimuli and their perceptual correlates. An overview of arguments used in favor of the dissociation between action and perception in normal subjects can be found in, for example, Goodale and Haffenden (1998) and Goodale and Humphrey (1998). In these studies, perception and action were based on visual or auditory information and action concerned movements of the hand. Franz, Gegenfurtner, Bülthoff, and Fahle (2000) criticized the experimental paradigms used in the previous studies, claiming that the results were experimental artifacts. In another study, Franz, Gegenfurtner, Bülthoff, and Fahle (2001) concluded that there is no evidence for a dissociation of action and perception. Sheliga and Miles (2001, 2002) reported that perceived slant can influence vergence responses (see "Discussion").

We used the Werner illusion (Werner 1937, 1938) to examine a possible dissociation between information processing for visual perception and eye movements. Figure 1 demonstrates the Werner illusion in which the narrow test strip in the middle is perceived to have illusory slant due to the slant of the large surfaces flanking the test strip. In this visual stimulus, the slant indicated by the size differences between the half-images (binocular disparity gradient) is different from the slant indicated by texture and perspective. Van Ee, Banks, and Backus (1999a) showed that the Werner illusion is due to the way in which the visual system reconciles the conflicting slant-cues, in combination with the preservation of relative slant between foreground and background (van Ee & Erkelens, 1996b).

In static viewing conditions, a change of direction of gaze is established by a very fast eye movement, called a saccade, which is (as is generally agreed) pre-programmed (Carpenter, 1988). This means that the new eye orientation is selected in advance. We examined whether

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(and if so, to what extent) binocular saccades are influenced by perceived slant. In Experiment I, the perceived slant was estimated using a psychophysical task. In Experiment II (consisting of two parts), eye movements were recorded while subjects made saccades between targets on the test strip. In the first part of this experiment (the "later saccades" experiment), the subjects were allowed to look around freely in the visual stimulus before recording began. Because visual feedback, present in free viewing conditions, might affect the saccadic properties, we carried out the second part of the experiment (the "first saccades" experiment) in which we concentrated on the first saccades following a period of strict fixation on the central target.

Methods

Apparatus

The visual stimuli consisted of stereograms that were presented dichoptically using conventional red-green anaglyphic filters. An HP 750 graphics computer generated the stereograms at a frequency of 70 Hz. These stereograms were back-projected on a fronto-parallel translucent screen (77 x 65 deg) by a D-ILA projector (JVC DLA-G11E). Subjects viewed the stereograms in an otherwise dark room, because visible frames of reference might reduce the Werner illusion. The viewing distance was 150 cm.

Visual Stimulus

Figure 1 depicts the stimulus containing three rectangular shapes presented at different heights with small gaps in between. The rectangle in the middle, called the test strip, was presented at eye level. The two larger flanking rectangular surfaces, which were presented above and beneath the test strip, together formed the background. Both the test strip and background consisted of sparsely distributed squares of 1.3 deg and 1.5 deg, respectively. The distribution of the squares was such that they covered about 70–80% of the stereogram. Presented in the test strip area were three targets (0.6 deg 'X' symbols) that were used in the experiment, described later, when eye movements were recorded. The subjects were positioned in front of the central target, which was located at the center of the screen. The other two targets were placed symmetrically about the subject's median plane at –15 and +15 deg of version. The targets were visible throughout each trial.

Horizontal scale-transformations (a disparity gradient) could be applied between the red and green half-images of the background and the test strip. From a geometrical

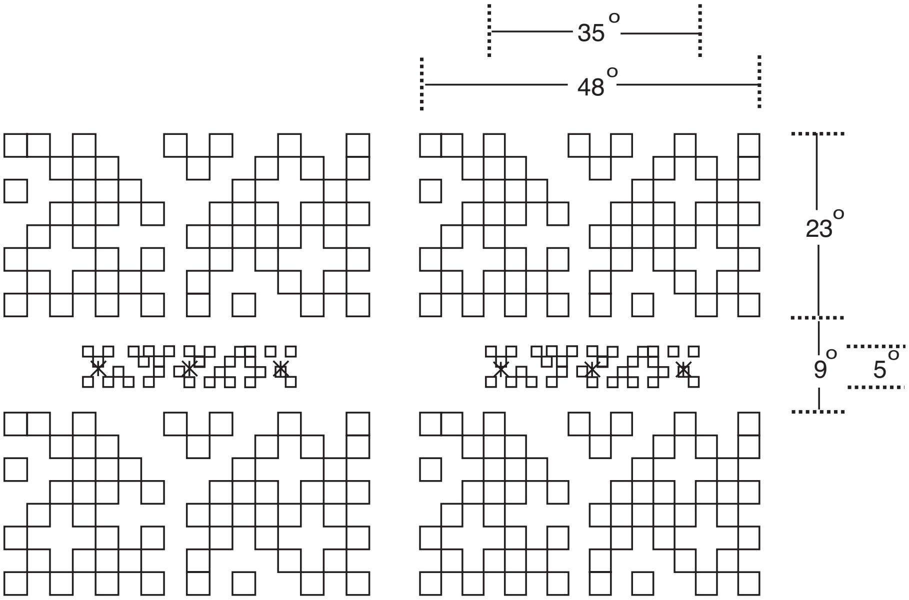

Figure 1. This stereogram depicts the Werner illusion. The narrow middle strip, called the test strip, is vertically flanked by two relatively large planes, together forming the background. The width of the background plane in the two half-images is different from each other (it is larger in the left half-image than in the right half-image), so the background ought to appear slanted. The widths of the test strip in each half-image are identical, so this test strip ought to appear unslanted. The Werner effect can be experienced when the two half-images of the stereogram are being fused: cross fusion gives the impression that the right side of the test strip is nearer than the left side, whereas the background appears to be almost fronto-parallel. Uncrossed fusion gives the impression that the left side of the test strip is nearer. The sizes are given for the unslanted planes and refer to those used in the experiments. The crosses represent the three fixation targets. Note that the dimensions are not to scale.

point of view, horizontal scale-transformations mimic surfaces that have slant about a vertical axis. A surface of which the right side is at a greater distance from the subject than the left side was defined to have positive slant. Unequal scale-transformations between the half-images for background and test strip produced a relative slant between the planes.

Three different test strip scale-factors were used, which led to geometrical test strip slants of approximately −60, 0 and +60 deg. The geometrical background slant ranged between −68 and 68 deg. Both slants are given relative to the frontoparallel plane (which has a slant of 0 deg). The positions of the three targets were scaled in the same way as the test strip so that the targets were seen in the plane of the test strip. The central target was always presented with zero disparity (i.e., at the screen distance).

Subjects

Three observers participated: AK (aged 26 years), CE (aged 51 years), and MB (aged 28 years). They had normal or corrected-to-normal vision, and they completed a metrical stereo test (van Ee & Richards, 2002). The subjects also completed a fixation disparity test described in Van Ee, Banks, and Backus (1999b).

Experiment I

In the first experiment, the task of the subjects was to estimate the perceived slant of the test strip. The slants were presented in random order, each stimulus containing a new distribution of squares of which one example is shown in Figure 1. The presentation period of each test trial was unlimited, and subjects could terminate the presentation when they felt ready to respond. After each presentation, two binocularly visible lines (one fixed and one rotatable) appeared on the screen. In a symbolic top view, the fixed line represented the median plane, and the rotatable line represented the orientation of the test strip. We explained the meaning of each line in the symbolic top view to the subjects. They were instructed to rotate the adjustable line, by changing the computer-mouse position, such that its orientation matched their perceived test strip slant (van Ee & Erkelens, 1996a). We explicitly checked whether they understood the instructions.

Experiment II

In the second experiment, we investigated saccadic eye movements made between targets on the test strip. Saccades were made between pairs of targets, one of which always was the central target, and the other was at either −15- or +15-deg eccentricity. A metronome was used to help subjects fixate each target for approximately 1.5 s. We used the following nine combinations (test strip slant, background slant): three non-illusory slant conditions (60°, 0°), (0°, 0°), (−60°, 0°), and six illusory slant conditions (60°, 60°), (60°, 68°), (0°, −60°), (0°, 60°), (−60°, −60°), and (−60°, −68°). These combinations were chosen on the basis of the responses in Experiment 1, so that the perceived slants for one geometrical test strip slant were as different as possible and also had opposite signs. Stimuli were presented in random order, each consisting of a new distribution of squares. The screen was blanked between trials.

Horizontal and vertical movements of both eyes were recorded using induction coils mounted in scleral annuli in an a.c. magnetic field as first described by Robinson (1963) and refined by Collewijn, Van der Mark, and Jansen (1975). The subject's head movements were minimized using individual dental bite-boards. Eye orientations were recorded with a frequency of 500 Hz. All data-analysis was done offline. The raw recordings were calibrated[1] using nine points at known visual angles at which the subject fixated (binocularly). Because the targets in the test strip appeared in the horizontal plane at eye level, the eye movements can be described by the longitudinal angles of the left and right eye. The version angle, given by the mean of the left and right eye orientation, indicates the binocular viewing direction. Saccades were detected using thresholds in the version velocity signal to mark onsets and offsets of saccades. The version velocity threshold was 50 deg/s, and the version velocity had to exceed this threshold for at least 6 ms. Saccades that contained blinks (on visual inspection) were not used in the data analysis.

Primary Saccades and Fixation

When subjects changed their direction of gaze, usually a large saccade was made first that covered the greatest part of the total version angle between initial and final target. This *primary saccade* was then followed by smaller correction saccades that brought the fovea onto the target. For each saccade, we subtracted the vergence angle (left minus right eye orientation) at saccadic onset from the vergence angle at saccadic offset (see Figure 2). This vergence difference will be called the intra-saccadic disconjugacy (ISD). The subject fixated the target in the interval 1200–1500 ms after the primary saccade. This was followed by a saccade to the central target. We averaged the vergence angle over the interval 250–0 ms prior to this centrally directed saccade to obtain the eye orientation during fixation on the target. We defined the intra-fixation disconjugacy (IFD) as the difference between this mean vergence value and the vergence at primary saccade onset. The vergence differences ISD and IFD are shown for one saccade-fixation sequence in Figure 2. The calculated IFD and ISD depend on the following factors: subject, leftward or rightward saccade, geometrical slant, and perceived slant (geometrical background slant).

In the following, we will distinguish “later saccades” from “first saccades”; these were recorded in two separate experimental sessions. The “later saccades” were made after a period of free viewing. For the “first saccades,” subjects fixated the central target before making the saccade to the eccentric target. This distinction enabled us to examine whether visual feedback (information about fixation errors at saccadic offset) would play a role for a possible effect of perceived slant on saccadic eye movements.

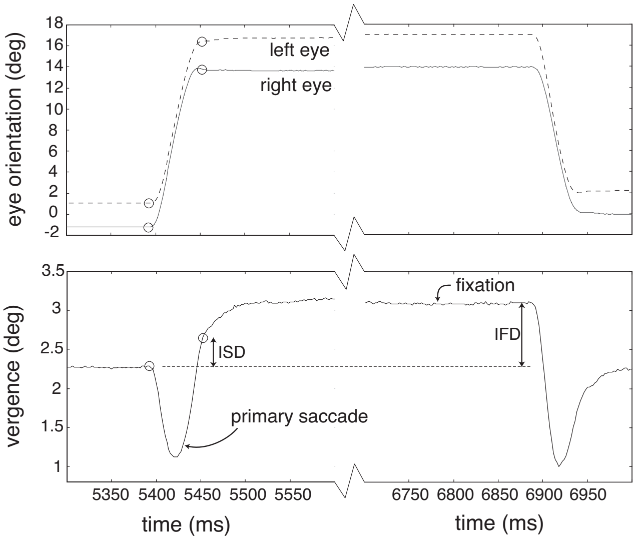

Figure 2. An example of one saccade-fixation sequence made by subject AK for the non-illusory slant condition (test strip slant, background slant) = (-60°, 0°). The top panel shows the left and right eye orientation; the bottom panel shows the vergence (left minus right) as a function of time for the same time interval. The circles mark the onset and offset of the primary saccades, which were based on version velocity thresholds. Note that saccades started at the center of the screen. This particular saccade went to the right target. The intra-saccadic disconjugacy ISD is specified by the difference between the vergence at the end and beginning of the first saccade. The intra-fixation disconjugacy IFD is specified by the difference between the vergence angle during fixation on the target and the vergence at primary saccade onset. A negative (positive) IFD value indicates that fixation is behind (in front of) the screen. A negative (positive) ISD value indicates a divergent (convergent) saccade.

Results

Results of Experiment I

In Figure 3 the perceived test strip slant is plotted as a function of the background slant for the three different geometrical test strip slants. The figure shows that the

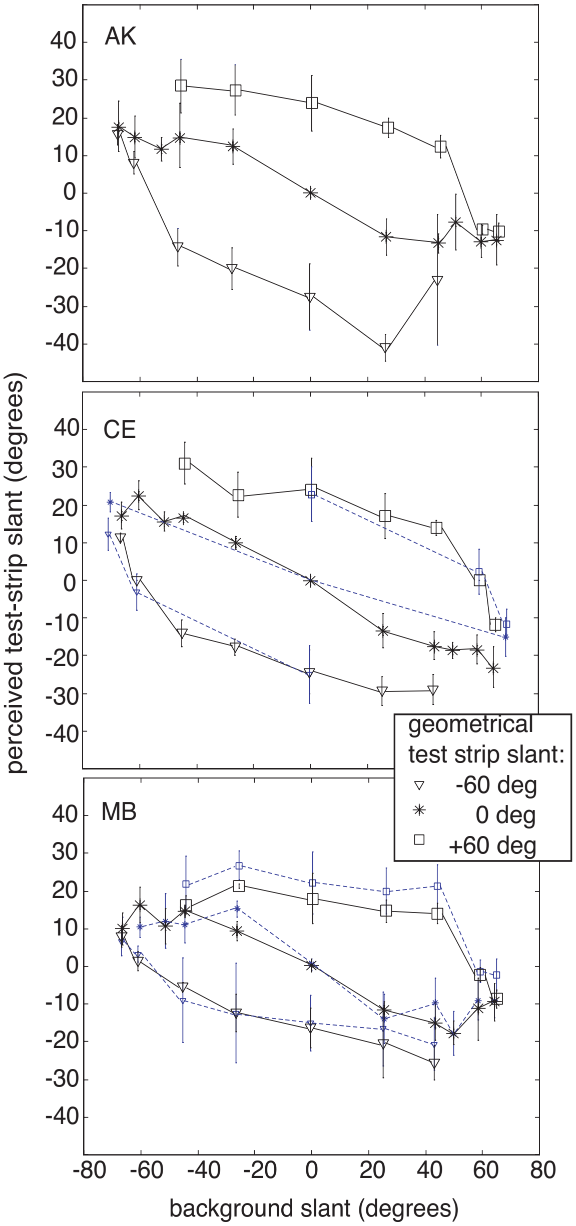

Figure 3. The perceived test strip slant is given as a function of the background slant for the geometrical test strip slants -60°, 0°, and 60°. The data show the mean of six settings for each condition, the error bars indicate ±1 SD. Not all combinations of geometrical test strip slant and background slant were fusible, so some combinations are absent. The presence of the background slant alters the perceived test strip slant for the three subjects in a similar way: it is mainly the relative slant that is perceived and this slant is assigned primarily to the test strip. Note the considerable underestimation; the perceived slant values -60° and +60° are outside the span of the *y* axis. These results were used in Experiment II: the solid lines were obtained using unlimited presentation time (part one “later saccades”); the dotted lines were obtained using a presentation time of 1.5 s (part two “first saccades,” subjects CE and MB only).

perceived test strip slant depends on the background slant. The estimated slant of the test strip decreases when the background slant increases. We can explain this finding by assuming that subjects primarily used the angle between the background and test strip for estimating the rotation angle of the test strip (Van Ee & Erkelens, 1996b) (i.e., the background was perceived to be more fronto-parallel than it should be from a geometrical point of view). Furthermore, all subjects underestimated the slant considerably. This underestimation is due to the monocular depth cues (that are crucial to produce the Werner illusion; van Ee, Banks, Backus, 1999a), indicating that the planes are fronto-parallel.

Results of Experiment II

"Later Saccades"

Here we focus on the "later saccades"; the next section is concerned with "first saccades." In the "later saccades" experiment, the subject was allowed to look around freely in the image *before* eye movement recording started. During recording, subjects had the specific task of making repeated saccades between the central target and the eccentric target. Each trial took about 30 s, during which time 14 saccades were made, 7 in each direction.

Figure 4 shows examples of the saccadic trajectories in terms of version angles and vergence angles for subject AK. In the middle row of Figure 4, it can be seen that the subject perceived the test strip as unslanted, which would require purely conjugate saccades. The trajectories show this did not happen, indicating that perceived slant did not drive the saccades. However, a small effect seems to be present in the third row. There is a visible tendency for the subject to follow perceived slant for the *rightward* saccades (no effect is visible for the *leftward* saccades). The eye orientation at saccadic offset is located somewhat nearer the subject than in the two other conditions. This could have been an effect of perceived slant because the subject also indicated (see third row left) that he perceived the right side of the test strip to be nearer.

The subjects could fixate the target for up to 1500 ms, which is enough to optimize fixation eye orientation and thereby to relate it to the geometrical location of the target in the best possible way. Although an effect of perceived slant on the IFD values would seem unlikely, the possibility ought to be examined; therefore, we tested whether there was an effect of perceived slant on the eye orientation during fixation (IFD) on the target. Then we examined the ISD values to test whether perceived slant has an influence on the intra-saccadic disconjugacy of saccades.

Results of IFD for "Later Saccades"

We calculated the predicted IFD values for each condition on the basis of the geometrical properties of the test strip slant. The predicted IFD values of the two eccentric targets for a geometrical test strip slant of 0° are –0.16°. For a geometrical slant of +60°, the IFD prediction for the left (right) target is 0.87° (–1.20°) and

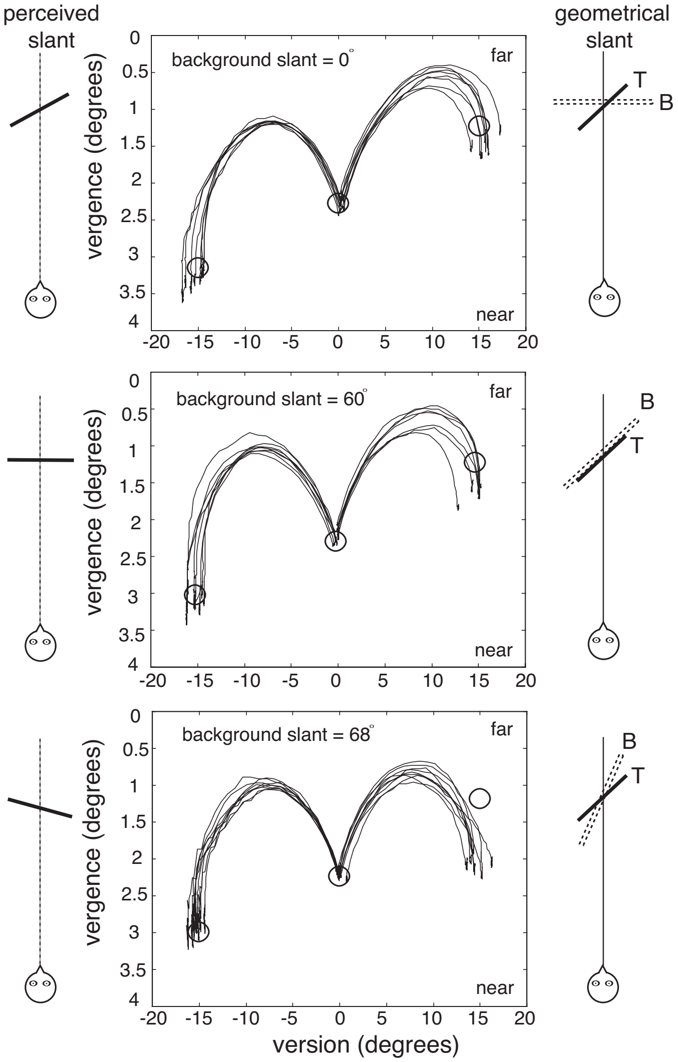

Figure 4. The saccadic trajectories of subject AK given in terms of version and vergence for "later saccades" in the interval from 120 ms before onset to 120 ms after offset. The test strip had a geometrical slant of 60 deg; the slant of the background was 0, 60, and 68 deg in the top, middle, and bottom row, respectively. The geometrical slant of both the background (B) and test strip (T) are shown on the right. The perceived slant of the test strip is given on the left. The locations of the targets, as specified by the geometry of the test strip, at –15-, 0-, and 15-deg version, are indicated by the circles. Zero-vergence angle implies fixation at infinity ("far"), and large vergence angles indicate near fixation ("near"). The saccadic trajectories are fairly similar irrespective of perceived slant. This suggests that the saccades are mainly, but not entirely, based on disparity information.

vice versa for a geometrical slant of −60°. These values depend on the subject's inter-ocular distance and are given for subjects CE and MB (io.d. ≈ 62 mm). The predicted values for subject AK are −0.14°, 0.74°, and −1.03°, respectively. Figure 5 shows the calculated IFD values (mean of 7-10 fixations for each condition) as a function of perceived slant for subject AK from his recorded eye orientations. These data show fixations on the right target for all nine slant conditions. The perceived slant was obtained from AK's responses in Experiment I. Figure 5 shows that the different geometrical test strip slants produced different eye orientations, which were close to the predicted IFD values (horizontal dotted lines).

For each set of data with the same geometrical test strip slant (these sets are indicated in the figure by rectangles, stars, and triangles), we compared the IFD responses of each illusory condition with the non-illusory condition of the same set. In this and the following data analyses, we used one-way ANOVA (with a 95% confidence interval) to examine whether responses of illusory slant conditions were significantly affected. We found two significant effects of which one could be caused by perceived slant (data with the black dot) but the other could not (the black triangle). As Figure 5 explains, the contribution of perceived slant was small relative to that of the disparity information.

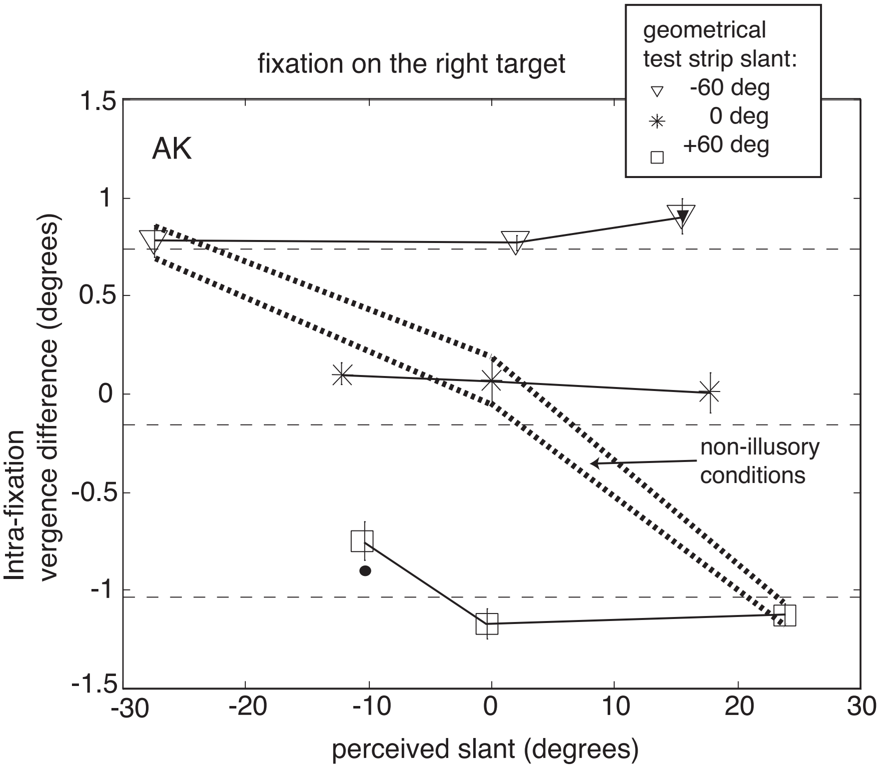

Figure 5. The intra-fixation disconjugacy (IFD: mean of 7-10 saccades) as a function of perceived slant for subject AK. We used the same symbols (triangles, stars, and squares) as in Figure 3 to indicate data belonging to a particular geometrical test strip slant (connected by the thin lines). The horizontal thin dotted lines give the IFD values predicted by the geometrical test strip slants. If, on the one hand, fixation eye orientation is determined by disparity information alone, the measured data for conditions with a particular geometrical test strip slant should be identical. Significant effects (one-way ANOVA, 95% confidence interval) were found for two of the illusory conditions. Only one of these effects can be explained by perceived slant (the rectangle with the black dot); the other is in the incorrect direction (black triangle). Furthermore, to obtain an indication of the contribution of perceived slant on the IFD responses relative to that of disparity information, we compare the data of illusory slant conditions with data of the non-illusory slant conditions. The thick dotted lines are obtained by connecting the error-bars (68% of the data lies within 1 SD for normal distributed data) for the non-illusory conditions: (test strip slant, background slant) = (60°,0°), (-60°,0°) and (0°, 0°). If perceived slant would have determined the IFD responses, all data would be located between the thick dotted lines (because these connect data for cases where perceived slant and disparity information are in accordance with each other). The significantly affected data lies well outside the thick dotted line area, implying that perceived slant has only a slight effect on subject AK's IFD values for fixation on the right target.

Figure 6 shows the IFD values for all subjects. The results of Experiment I were used to obtain mean perceived test strip slants for each combination of geometrical test strip and background slant. Because subjects were allowed to look around freely in the image before recording began, we did not measure perceived slant in the “later saccades” experiment but used the results obtained in Experiment 1, where subjects were also allowed to look around freely. For the IFD responses of Figure 6, we found significant effects in seven of the 36 illusory slant conditions. Of these seven, six could be explained as an influence of perceived slant. Perceived slant had no effect on MB, CE showed an effect in four conditions, and AK in two conditions. As Figure 6 shows, this influence of perceived slant on the IFD data was small compared to the contribution that disparity information had on the non-illusory conditions.

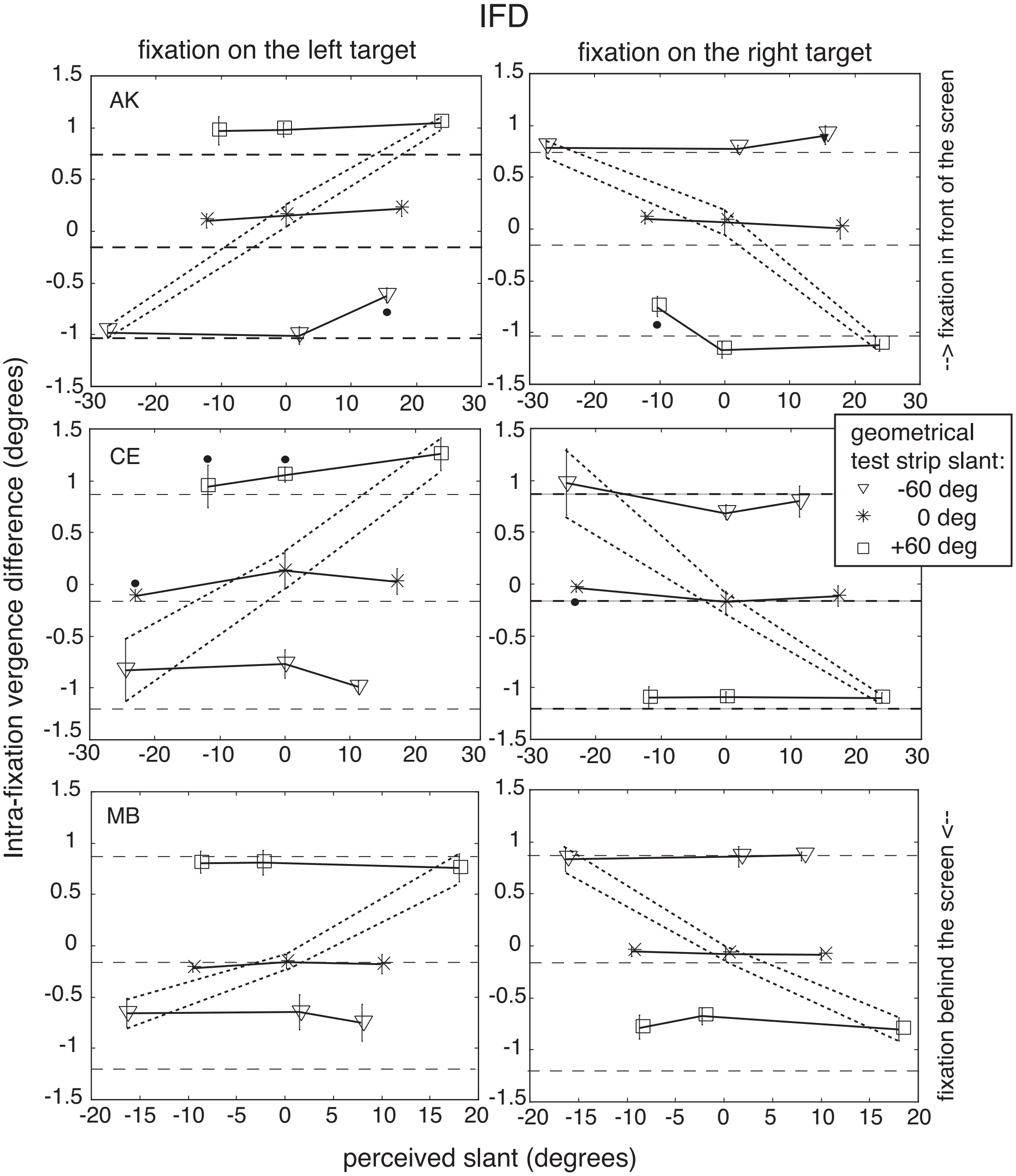

Figure 6. Same as Figure 5 for the three subjects (the top right panel is Figure 5). Fixations on the left (right) target are given in the left (right) column. In 6 out of the 36 illusory slant conditions, a small effect of perceived slant is visible (data marked by black dots). In the majority of cases, illusory slant shows no significant effect on fixation eye orientation. The single symbol (top right panel) with a black triangle indicates unexplained data.

Results of ISD for “Later Saccades”

Next we examined the effect of perceived slant on the intra-saccadic disconjugacies (ISD) (i.e., on the primary saccades). It is possible that the visual system takes the perceived slant into account in the preprogramming of the saccades, together with the actual disparity information.

Figure 7 shows mean values of the calculated ISD values (7–10 saccades for each condition) for “later saccades” as a function of perceived slant. The calculated ISDs are in general different (or they even have a different sign) from the values predicted on the basis of disparity information. This is due to the transient divergence that is present in binocular saccades. We compared the calculated ISD values with each other in the same way as we did in Figure 5. The ISD values differed across subjects. For example, subject CE made predominantly divergent saccades (negative ISD), whereas subject AK and subject MB made both divergent and convergent saccades. In Figure 7, we find a significant effect on ISD responses for 19 of the 36 illusory conditions (10 of 12 for subject AK, 6 of 12 for subject CE, and 3 of 12 for subject MB). Three of the significant results of Figure 7 do not seem to be produced by disparity information or

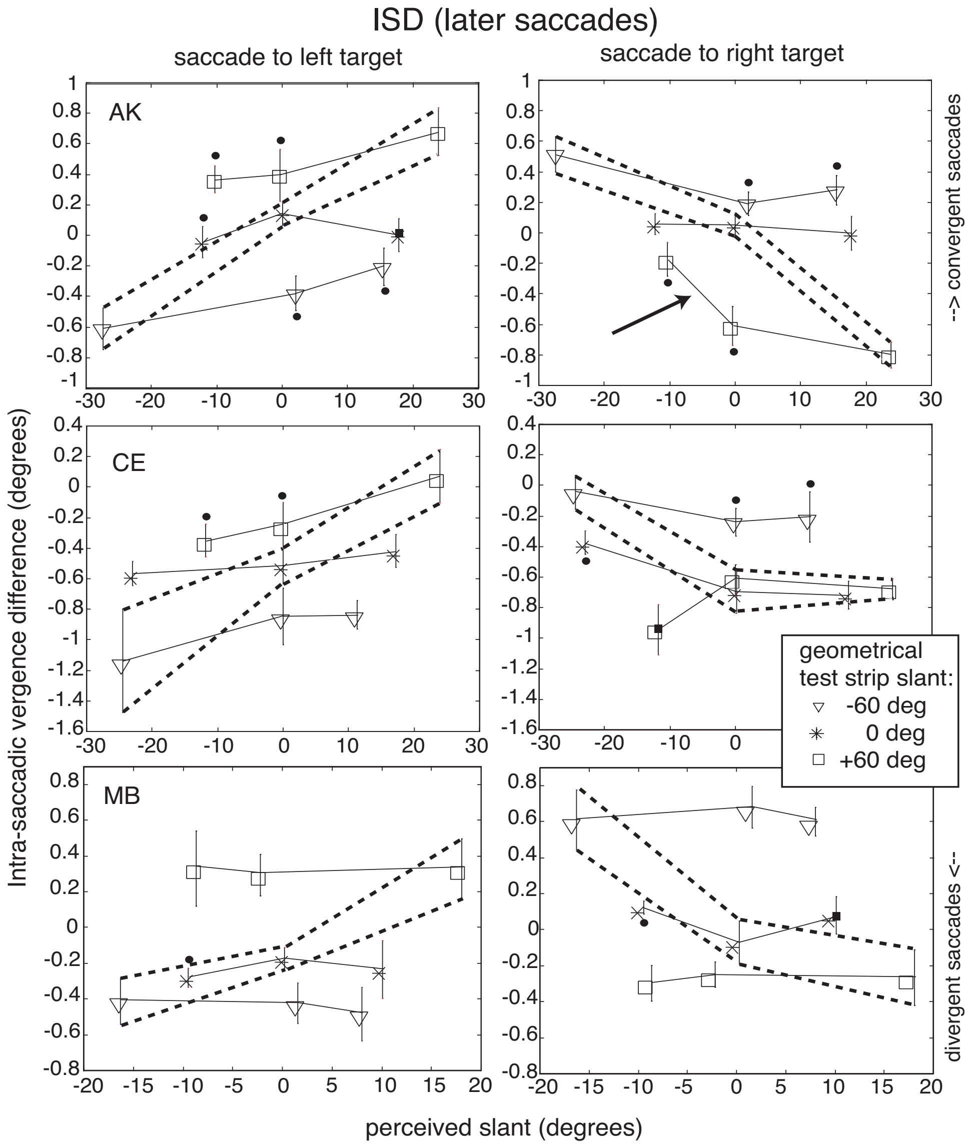

Figure 7. Similar to Figures 5 and 6, but now for intra-saccadic disconjugacies (ISD) as a function of perceived slant for “later saccades.” Results of leftward (rightward) saccades are given in the left (right) column for the three subjects. Note that the vertical scales in this figure are different across the three subjects, and they are also different from those used in Figure 6. The rightward saccades of subject AK in Figure 4 are represented by the data of the bottom thin line in the top right figure (to which the arrow points). A significant effect of perceived slant on the intra-saccadic disconjugacy is present in 16 of the 36 illusory slant conditions (data marked by black dots). The symbols with a black square indicate unexplained data.

by perceived slant: these data are indicated by black squares. Of the 36 illusory slant conditions in Figure 7, three unexplained results are present, 16 were influenced by perceived slant, and the remaining 17 conditions were determined solely by disparity information. So the first part of Experiment II shows that perceived slant does influence the intra-saccadic disconjugacy when saccades are made after a period of free viewing.

“First Saccades”

To examine whether visual feedback (present under free viewing conditions) plays a significant role in our findings for the first part of Experiment II (concerning the intra-saccadic disconjugacy of primary saccades), we conducted the second part of Experiment II, in which the feedback was absent. We were interested primarily in whether the influence of perceived slant on the ISD was larger in the absence of visual feedback. In this “first saccades” experiment, subjects were required to strictly fixate the central target before making one saccade to either the left or right target (so they were not allowed to look around as in the “later saccades” experiment). Each trial started with the presentation of only the central target that had to be fixated.[2] This was followed by the presentation of the complete Werner stimulus. After a fixation period of 1.5 s on the central target, in which the slant of the test strip became apparent[3] to the subject, a saccade was made to either the far left (–15 deg version) or far right (+15 deg version) target. Then the screen blanked, and the central target re-appeared for the next “first saccade” recording. For each combination of geometrical test strip slant and background slant, a total of seven “first saccades” in each direction were recorded for subjects CE and MB.

The same data analysis was used as in the previous experiment. We focused only on the analysis of ISD: because fixation involved visual feedback for up to 1500 ms, analysis of the IFD should give similar results in both the “later” and “first saccades” experiments. Indeed, we found no effect of perceived slant (no figure is shown) on the fixation characteristics in the “first saccades” experiment.

Results of ISD for “First Saccades”

Figure 8 gives the calculated ISD values for “first saccades” (7–8 saccades for each condition) as a function

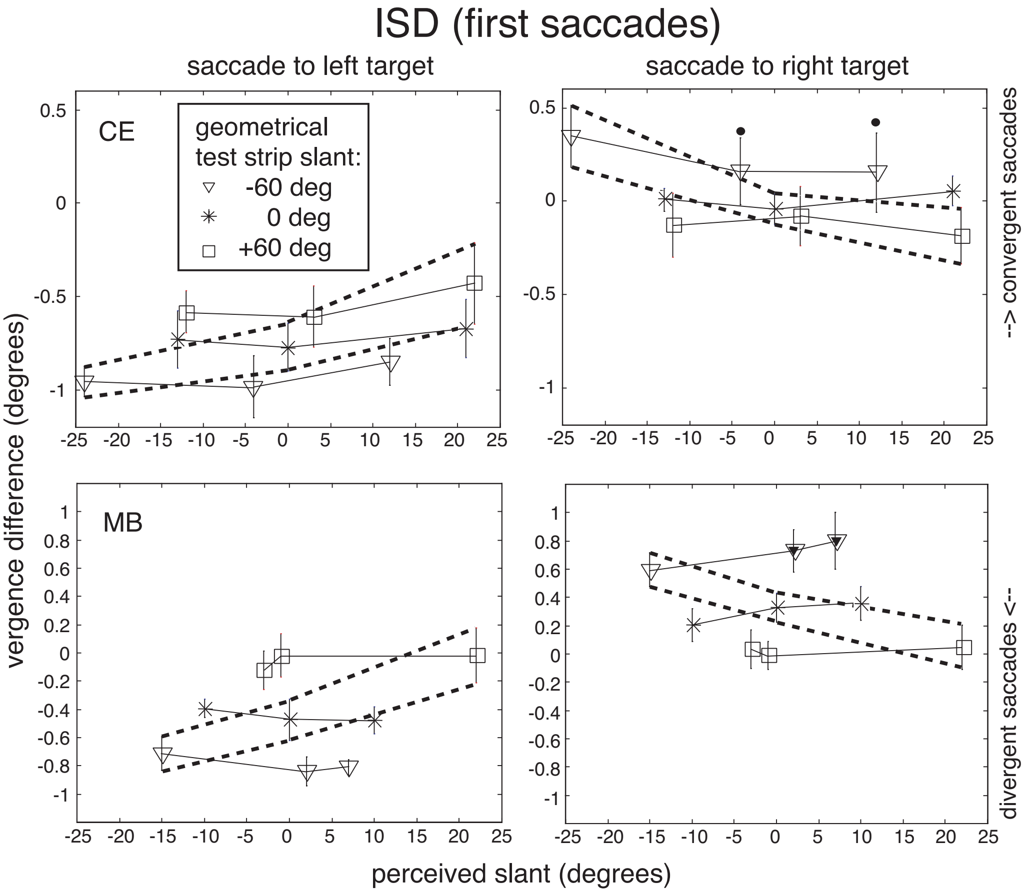

Figure 8. Same as Figure 7 but for “first saccades” of subjects CE and MB. The ISD values are based on the mean of 7-8 saccades. In two cases, the effect is in the wrong direction (marked by the black triangles in the bottom right panel). In two of the 24 illusory slant conditions (marked by black dots), there is a significant effect of perceived slant on saccades.

of perceived slant. To obtain the mean perceived slants for each combination of geometrical test strip and background slant, we used the results of Experiment I (the dotted lines in Figure 3). In order to verify that the perceived slant, before the "first saccades" were made, was the same as found in Experiment I, subject CE reported his perceived slant while he fixated the central target. His estimations under strict fixation were very similar to the estimations he made while freely making scanning eye movements in Experiment I (see also Van Ee & Erkelens, 1999, who found similar results). The perceived slant of subject MB for the "first saccades" was estimated using the same adjustment procedure as in Experiment I, with the exception that the subject had to fixate the central target during the short presentation period of 1.5 s. As Figure 3 shows, this subject was also capable of perceiving the (illusory) slant within the required time.

The ISD responses between the non-illusory slant conditions for the "first saccades" did not differ as much as for the "later saccades." This already indicates that perceived slant could not have played a large role in the ISD responses of "first saccades." Subject CE's rightward saccades depicted in Figure 8 do show a significant influence of perceived slant in two illusory conditions. Subject MB's data show no influence of perceived slant: the two significant effects for this subject are in the wrong direction. So two out of the 24 illusory slant conditions show an influence of perceived slant in the absence of visual feedback.

Discussion

To study a possible dissociation between action (binocular saccadic eye movements) and perception (perceived slant), we investigated whether saccades are determined solely by geometrical slant or whether they are influenced by both geometrical and perceived slant. Our results show that the intra-saccadic disconjugacy is determined in the first place by disparity. Perceived slant seems to have only a slight influence on the binocular saccades.

Binocular Viewing

The generation of binocular saccades of unequal sizes is a normal feature of oculomotor performance whenever gaze shifts between targets differ both in direction and depth (Erkelens, Steinman, & Collewijn, 1989). Retinal stimuli that contain disparity represent objects of the three-dimensional environment from a geometrical point of view. However, the monocular depth cues, such as perspective, do not necessarily support the depth specified by the disparity. Kapoula, Eggert, and Bucci (1995) examined how rapidly normal subjects were able to alter the conjugacy of their binocular saccades in a more artificial cue conflict situation in which a rectangular grid in one half-image was 10% larger than that in the other half-image. Their study showed that saccades were immediately disconjugate for the majority of their subjects. However, the subjects did not perceive the disparity-specified slant. In accordance with our results, they showed that the (absence of) perceived slant does not drive conjugate saccades if disparity requires *dis*conjugate saccades. Erkelens and Collewijn (1985a) showed that equal and opposite motions of two large half-images constituting a random-dot stereogram, viewed without a frame of reference, are perceived as a stationary, fused image in constant stereoscopic depth. Erkelens and Collewijn (1985b) measured smooth pursuit to these visual stimuli and showed that the vergence was modulated, although no motion in depth was perceived. These studies show that disparity can elicit vergence movements (both smooth and during saccades) in the absence of the appropriate percept. In other words, these studies show no evidence that perception was used for eye movements during binocular viewing; eye movements were driven by disparity.

A study in this issue of the *Journal of Vision*, by Sheliga and Miles (2003), reports that perceived slant can significantly influence vergence responses even in open-loop conditions. Sheliga and Miles (2003; see also 2001, 2002) used Ogle's induced effect to dissociate the perceived slant from the slant specified by horizontal disparity. In the induced effect, an unslanted flat surface in the frontal plane appears slanted about a vertical axis when the image in one eye is vertically magnified. They found for this situation that open-loop gaze shifts between targets located on the surface were accompanied by changes in the horizontal vergence angle (whereas horizontal disparity would predict no changes). They also asked subjects to apply vertical compression to one eye's image to null the perceived slant resulting from horizontal compression, and then they recorded the vergence eye movements during open-loop horizontal gaze shifts. For this condition, too, they found that perceived slant influenced vergence angles. They estimated that perceived slant accounted for up to 41% (condition dependent) of the vergence changes in their experiments.

What could explain the difference between their strong effect and our weak effect of perceived slant? First, it might have been due to procedural differences. They studied open-loop responses. Our ISD-analysis compares best to their work. In this analysis, we studied the initial portion of the vergence response (which does not permit closed-loop processing). Ideally one would like to replicate our Werner-effect study with their procedure. However, although this might explain a part of the differences, we feel that it is unlikely that this will account for all of the large differences. Second, it might be due to stimulus differences. The visual slant cues provided by Werner's slant contrast illusion and Ogle's induced effect are different, and one could state (as Sheliga and Miles explicitly did) that in some of their experiments, the slant specified by monocular cues is consistent with perceived slant, whereas it is inconsistent in our experiment. Although the role of monocular cue conflict is not clear in the generation of saccades, this, too, is unlikely to explain all of the differences because they also found an effect of perceived slant when there was a nonzero vertical disparity gradient (nonzero slant) and zero horizontal disparity gradient. As they pointed out themselves, this rules out cue-conflict as an explanation for their large effect. So, this does not explain the conundrum either.

This leaves us with one other not directly obvious—but yet possible—suggestion that requires further research. In each of Sheliga and Miles' conditions in which perceived slant influenced the vergence, there was always a vertical disparity gradient present. In our experiment, we neither manipulated the horizontal disparities of the surface, nor did we manipulate the vertical disparities. So, although it is relatively unlikely to be the case, theoretically there is the possibility that in Sheliga and Miles' experiments, it is not perceived slant but the co-varying vertical disparity gradient that influenced the vergence responses. In order to control for this possibility, one needs a stimulus with only a vertical disparity gradient (and no horizontal disparity gradient), such as is present in a stimulus consisting of long horizontal lines. We do not know of any study that has investigated whether a pure vertical disparity gradient can affect horizontal vergence responses associated with horizontal saccades. Such a control could help in resolving the differences between our findings.

Monocular Viewing

Is saccadic disconjugacy related purely to the disparity information or is it also produced by the monocular (depth) content of the image? The following studies examined whether pictorial depth can produce appropriate intra-saccadic disconjugacy for binocular eye movements during *monocular* viewing. In two studies by Enright (1987a, 1987b), the subjects monocularly viewed paintings with strong perspective cues to depth. Saccades made between targets at different locations showed disconjugacy in the direction implied by the perspective cue in the image. Ringach, Hawken, and Shapley (1996) showed that the perception of three-dimensional structure from monocular two-dimensional images changing over time-the kinetic depth effect (KDE)-can evoke binocular eye movements consistent with a three-dimensional percept. Monocular tracking of a small patch on the three-dimensional object produced smooth pursuit eye movements, containing a vergence component that changed with the implied depth. These studies show that there is a strong association between depth perception and eye movements (for both saccades and smooth tracking) when viewing is monocular.

Depth Cue Conflicts

The above-mentioned studies did not examine situations in which the depth defined by disparity conflicted strongly with the depth produced by monocular cues. We showed that in such large cue-conflict situations, the main source for the intra-saccadic disconjugacy is the disparity information. However, we also showed that in some cases the perception-associated disconjugacy can affect binocular saccades. We argue that the influence of illusory (monocularly perceived) slant that we measured in the present study is caused by the effect we just mentioned for monocular viewing. This idea is consistent with findings of Bucci, Kapoula, and Eggert (1999). They (see also Eggert, Kapoula, & Bucci, 1994) presented subjects with three different images (a random-dot stereogram, a grid, and a complex image, containing various monocular cues to depth), each having the same disparity (10% uniform magnification). Their data show that different disconjugacies were produced in response to these stimuli. The response to the random-dot pattern was the strongest and most persistent, that to the grid was smaller while that to the complex image was the most variable. Bucci et al. (1999) concluded that binocular saccades are different when the depth contents, based on monocular depth cues, of the images are different. However, it might be the case that the found intra-saccadic disconjugacy is based on the density of correlated features between the half-images (which is clearly different in a stereogram, a grid, and a complex image), and not on what is perceived. The advantage of using the Werner illusion in our study is that we kept the density of disparity information the same in each condition, and we were able to manipulate perceived depth by changing only the surround.

Conclusions

We conclude that binocular saccadic eye movements are determined predominantly by the geometrical properties of the stimulus but they can be affected by perceived slant, particularly when multiple saccades (i.e., visual feedback) are allowed. Findings so far are consistent with the general proposition that perceived depth can influence binocular saccades during viewing of depth illusions (although there is controversy as to the amount), and that the influence of perceived depth is most notably present in saccades during monocular viewing.

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Footnotes

[1] The calibration method took into account the distortion of visual direction caused by the glasses worn by subject MB and possible fixation disparities of subjects.

[2] All the experimental methods were the same as described in the previous section. The eye orientation data were later inspected to ensure that the subject carried out the task in this experiment correctly (i.e., the subject did not cast a quick glance at the target during this fixation period). No mistakes were found.

[3] Relative disparities produced perceived depth differences as soon as the subject fused the stereogram.

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